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L.M.B.C. MEMOIRS

ON TYPICAL BRITISH MARINE PLANTS & ANIMALS

EDITED BY
R. J. DANIEL, D.Sc.

XXXI.

MYTILUS

BY
KATHLEEN M. WHITE, B.Sc.
ZOOLOGY DEPARTMENT, UNIVERSITY OF READING

(With 10 Plates)

THE UNIVERSITY PRESS OF LIVERPOOL

MARCH, 1937

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EDITOR'S PREFACE

THE Liverpool Marine Biology Committee was constituted in 1885, with the object of investigating the fauna and flora of the Irish Sea.

Dredging, trawling and other expeditions, originally organised by the Committee, have been carried on intermittently since that time, and a considerable amount of material, both published and unpublished, has been accumulated.

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No. XXXI. MYTILUS

BY
KATHLEEN M. WHITE, B.Sc.
ZOOLOGY DEPARTMENT, UNIVERSITY OF READING.

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INTRODUCTION.

Mytilus edulis is a Lamellibranch mollusc belonging to the order Filibranchia, sub-order Mytilacea, family Mytilidæ.

The order Filibranchia is primarily separated from the other orders by the structure of the gills, which are in this case formed of parallel reflected filaments. The filaments are connected by cilia which occur in restricted patches on the sides of the filaments; that is, the interfilamentar junctions of the Filibranchia are ciliary. Another characteristic of the order is the presence of a well-developed byssus organ, which forms an attachment of a more or less permanent nature to a solid foundation.

Pelseneer (1906) divides the order into five sub-orders—Anomiacea, Arcacea, Mytilacea, Pectinacea and Dimyacea.

The Mytilacea are forms in which the anterior adductor muscle is smaller than the posterior adductor muscle (the anisomyarian condition), or else it is absent altogether. There are non-vascular junctions connecting the gill lamellæ. There is only one aorta, the anterior. The ramifications of the gonads usually extend into the mantle.

The members of the family Mytilidæ, d'Orbigny, have an inequilateral shell, the anterior side of which is very short. The ligament is external and true hinge teeth are absent. The mantle has one point of union which is situated posteriorly and separates the exhalent aperture from the rest of the pallial opening. Cephalic eyes are present.

Winckworth divides the British members of the family into five genera with fifteen or sixteen species. The genus *Mytilus* has two species, *Modiolus* (the horse mussel) has five or six, *Adula* has one, *Musculus* has four and *Crenella* three.

The genus *Mytilus* has an extremely inequilateral shell which is generally sub-triangular in shape. The beaks are terminal and the hinge, though not having true hinge teeth, is irregularly denticulated. The ligament is linear.

The two species of *Mytilus* are *M. edulis* Linné 1758, and *M. galloprovincialis* Lamarck 1819. The latter is a foreign introduction which should not be confused with the variety described by Jeffreys, which differs from *edulis* by having a broader and flatter shell, a more prominent ventral margin and incurved beaks. Its habits are different in that it is more or less solitary in occurrence and burrows in the mud. For the purpose of this memoir, *edulis* alone is described, but *galloprovincialis* (sp. or var.) can be substituted for dissection if it is so desired.

Mytilus edulis is a good type for a memoir in that it is easily obtainable and makes a straightforward subject for dissection. Economically the animal is very important, and it has been eaten for many centuries. Quoting Lovell, " Athenæus says that Mussels are moderately nutritious and digestible."

The word " mussel " is probably derived from the Anglo-Saxon *muscl, muscel, muscule, muscla,* and means that which instantly retires on being touched. This instant retirement is certainly a marked characteristic.

The Mytilacea are considered by Pelseneer to have given rise to the sub-Mytilacea on the one hand and to the Pectinacea and Ostreacea on the other.

HISTORY.

Mytilus edulis was described by Linnæus in 1758. He refers to the genus *Mytilus* as: "Animal Tethys. Testa bivalvis, rudis, sæpius affixa Bysso. Cardo edentulus, distinctus, linea subulata, excavata, longitudinali." *M. edulis* is the 215th species of his Vermes Testacea, and is described as: "M. testa læviuscula violacea, valvulis obliquis postice acuminatis."

The marine mussel was anatomised by de Heide in 1683. He first saw cilia and ciliary action in the gills of this animal in 1680. He describes most of the organs which would be visible in ordinary dissection, but does not mention the heart or nervous system, nor does he discuss the generation of the species. His account of the course of the gut is also not correct, but he discovered and named the crystalline style. Leeuwenhoek describes histological and other observations made on the species in five letters between 1686 and 1708. He also witnessed ciliary action in the gills, and apparently discovered the ciliary junctions in these organs. He believed that the eggs developed at first within the parent and were then deposited on the exterior of the shell by the foot. No males were found, although the male is the more numerous sex. The "eggs" which Leeuwenhoek described on the shell were the Polyzoan *Membranipora.* In 1696 Martin Lister found the heart, but did not understand its structure. The heart was correctly described for *Anodon* in 1712 by Mery. Lister accepts Leeuwenhoek's account of the generation of the species, as did H. Baker in 1742, and his anatomical description is based largely on de Heide and Leeuwenhoek. Baker describes the circulation of the blood in the mantle. It was not until 1761 that Leeuwenhoek's erroneous account of the generation was corrected by Baster. This author refers to the breeding season as the closed season in the Mytilus fishery, in order that there may be no impediment to their generation. Baster distinguished the sexes and saw the rod-like egg groups being discharged in the exhalent current and notes their subsequent dissolution into separate eggs.

Poli in 1795 attempted a more ambitious anatomy of the species. He found a part of the nervous system, but regarded it as a lymphatic apparatus. He described the gut correctly and noted that the ventricle of the heart was traversed by the rectum. He injected the blood vessels with mercury, but his account of them is imperfect and not easy to interpret. He did not see the kidney.

HABITAT.

Mytilus edulis is a very common littoral species. Specimens have been taken from deeper water, but are then much below average size. In Wembury Bay, 10 feet below low water, ordinary spring tide, very small individuals occur fixed to Laminarian holdfasts and to *Corallina*, with some specimens amongst the weeds. The usual habitat is from high-water mark to a few fathoms.

Mytilus edulis is tolerant of great variation in salinity and occurs in salt, brackish and in nearly fresh water. Adults are always attached by the byssus, or " beard," and are therefore not found on sandy shores unless there is some adequate supporting structure present. But where there are rocks, piles or piers anywhere round our shores *Mytilus edulis* is usually plentiful. Estuaries and harbours are common habitats.

Edible mussels are also abundant on the opposite shores of the English Channel, where they prefer, according to Boutan, the more recent rather than the older rocks. They do occur in Brittany, but flourish far better on the secondary rocks on the northern part of the coast. For instance, they are very large and plentiful around Boulogne.

When present at all, the mussel is usually abundant and a favourable locality will be completely covered with them, no free space being left for other attached organisms.

The byssus holds the animal very firmly to its substratum and considerable force is then required to remove an attached animal. When forced away in this manner, the byssus is either broken off from the attached surface or else it may be torn out from its own roots.

Johnstone says that the density of a bed may be as great as 16,000 mussels to the square foot but this is exceptional, and he also gives figures suggesting the frequency of the larvæ occurring in the plankton. In the Western Baltic, tow netting indicated that there were 170,000 larvæ per square metre of surface in a given area.

Frequently this extreme example of gregariousness is its own undoing. At St. Anne's-on-Sea the mussels settle down every two years on a gravel bed. Accumulations of mud and excreta form around and amongst them, and during the next two years the mass attains a depth of about 2 feet. Then heavy seas reaching the bed roll up the whole mass of mud and mussels like a carpet and break it to pieces on the foreshore. The molluscs are thus scattered. The recently cleared bed with its freshly exposed gravel is then repopulated, and so the alternation of formation and denudation of the mussel bed goes on. In other localities, where the wave action is not so violent, the mussel beds can be much more permanent, for when, under these circumstances, the accumulation of debris gets too great the animals can raise themselves by lengthening the byssus and can settle down again on the living and dead shells of their companions.

Mytilus edulis, although normally an attached form, is capable of locomotion. The animal can propel itself by the foot as do other molluscs, the method adopted being similar to that of the snail. Williamson says that young ones seem to travel with the anterior end foremost, while the reverse direction of movement is used by older individuals. Lang noticed a mussel climb up a perpendicular glass wall by attaching itself by means of the suctorial tip of the foot, lifting itself on the foot and then making a byssal thread fast. On the formation of a second thread above the first, the latter would be broken off, and so on. A sudden jerk of the foot is used to break the threads.

A considerable amount of slight movement in a limited area takes place by means of the byssal muscles, which can by their contraction and relaxation slacken or tighten the byssal threads. In this way jerky movements can be brought about within the limits of the thread. Williamson noticed that this was the way in which mussels remained covered for a longer period by receding water, being able to let themselves down into the water by the byssus.

Coultbard has made experiments upon *Mytilus edulis* to determine the effect due to variations in environmental factors. He found that medium sunlight and a temperature range between 10° and 20° C., were the optima for light and heat. (See RATE OF GROWTH.)

Dodgson notes that mussels have been seen to function with ordinary activity at temperatures between 0° and 26° C.

Bouxin has found that *Mytilus edulis* can respire normally in water varying from the average salinity up to an admixture of 30 per cent. fresh water or with an increase of salinity resulting from the addition of from 5 to 10 per cent. of water that has been concentrated to a salinity of 7 per cent. An increase of fresh water to 60 per cent. or an increase of salinity to 35 per cent. of added water which has been concentrated to 7 per cent. salinity kills the animal within a very short time. Between these wide limits, however, a considerable amount of variation occurs. Bouxin says, " these molluscs show an individual sensibility indicating an individual physiology " [trans.].

The vitality shown by mussels is considerable, especially by those taken from firm-bottomed grounds. Mussels can survive out of water for a longer period of time if they are kept dry, as in this case the shell is tightly closed, with sea water in the pallial cavity, but if damped they occasionally open and therefore allow this contained water to escape.

Dodgson reports that mussels have lived normally for over a month in sterile water ; that they have been found alive after twenty-four days in hot sun ; and that they showed movements of the adductor muscles after forty days of anaerobic conditions. This indicates the degree of vitality shown by the animals. Formation of the byssus falls off after the first day of this treatment.

FOOD.

Field has investigated the food of the mussel from specimens at Woods Hole, Massachusetts. In 1911 he named twenty-nine species of Diatoms and nine species of Protozoa which he took from the stomach of mussels, but later, in 1921–22, he found that these do not form more than about half of the bulk of food taken in, and that the other half, which consists of detritus, is probably of greater importance as food. Field is not alone in having neglected the nutritive importance of the detritus. It is, however, the detritus and the smaller plankton which is utilised by the animals, the rest being discarded as pseudo-fæces. (See **Feeding Mechanisms.**) Field found that the volume of material extruded daily by a single specimen as true fæces averages 40·8 c.mm. The amount taken in, of course, is probably considerably more than this. To obtain the food matter, as Dodgson calculates, a mussel filters 10 gallons of water in twenty-four hours. Jensen investigated the food value of detritus, and Blegvad emphasises the importance of detritus as food for Lamellibranch molluscs, regarding it as their principal food, and the value of the live phytoplankton as very slight. Jensen considered that in most of the seas round our shores the green plant *Zostera* is probably the principal source of the decayed organic matter of the sea bottom or detritus, though plankton contributes to it. *Zostera* is much richer in pentosan than is the marine plankton and is also rich in nitrogen, but there is more of this in the detritus than in the fresh *Zostera*, and Jensen found relatively more nitrogen in samples showing increasing degrees of decomposition. In the upper layer of the detritus there are from 44 to 68 mg. of digestible proteins per 100 sq. cm. Non-nitrogenous compounds contain a considerable amount (0·3 to 1·0 per cent.) of pentosan. Gastropods have been found to digest pentosan, so it is not improbable that further investigations will show this process to take place also in the Lamellibranchs. Blegvad says: "Detritus forms the principal food of nearly all the invertebrate animals of the sea bottom, next in order of importance being plant food from fresh benthic plants. The value of the live phytoplankton in this connection is absolutely minimal, amounting in any case to nothing more than an indirect significance through the medium of the plankton Copepods." Blegvad found that many members of the plankton can pass through the intestines of these animals without undergoing any change. He cites the case of *Procentrum micans*, which can pass alive through the gut of *Mytilus edulis*. Ciliary feeders such as *Mytilus edulis* obtain their food from the detritus suspended above the bottom, but the above-quoted workers assert that this has the same composition as the actual bottom detritus.

BIONOMICS.

The inter-relationships between *Mytilus edulis* and other species are considerable. The chief enemy of the mussel is the common star-fish, *Asterias rubens*. This opens the mussel shell by holding on to the two valves with the tube feet of all five arms. Sufficient pull is then exerted by the arms to overcome the resistance offered by the adductor muscles. This may take some time—hours or even days being occupied by the process—but the muscles usually relax in the end and the shell gapes. The echinoderm is then able to insert its stomach between the valves of the shell and consume the mollusc. The dog whelk, *Nucella lapillus*, also eats *Mytilus edulis*. It bores a hole, usually $\frac{1}{16}$ of an inch in diameter, with its radula, and through this hole, which is generally circular and always smooth in outline, the proboscis is pushed. *Urosalpinx cinerea* behaves in the same way.

Other enemies are birds, principally the herring gull, wild duck and oyster catcher, and fish, notably eels (according to Blegvad), while plaice, dabs and flounders attack the young mussels. Field quotes Dycke in saying that *M. edulis* is the sole food of the walrus. As well as these active enemies, there are a considerable number of passive ones which become a menace if their numbers increase much. Of these there is the eel grass, *Zostera marina*, also *Fucus vesiculosus* and other Algæ; the Molluscs *Crepidula fornicata* and *Anomia* spp.; Ascidians, Sea Anemones and Hydroids, Sponges and Barnacles. All of these can damage or destroy the mussel beds by either choking them or eating the food. *Zostera* in particular never forms a favourable habitat, whereas *Fucus*, if not too abundant, supplies a useful shelter.

Sand may be included in the category of passive enemies, as silting up by sand or mud may cause the partial or complete destruction of mussel beds. In connection with the harmful effects of sand, Wright mentions that sand with shingle may cause erosion of the shells to the extent of wearing away part of the two outer shell layers. Barnacles, though included as passive enemies, are frequently advantageous rather than destructive to mussels. Rocks with a good incrustation of barnacles afford a rough surface of attachment which is very suitable for the young individuals, many of which can also be found occupying the empty shells of dead barnacles. Wright has found cypris and nauplius stages of the barnacle in the stomachs of mussels.

As a commensal, there occurs in the mantle cavity of many adult *Mytilus edulis* which occupy healthy surroundings the small pea-crab, *Pinnotheres pisum.* It is apparently harmless, but its stomach has been found to contain diatoms and other food substances of the mussel and, therefore, by depriving the mollusc of some of its food may affect its growth. If the crab is very large it may harm the mollusc by exerting pressure on various organs, chiefly the mantle. Where this is the case, the nacreous layer is worn away, and this, as Wright suggests, may be due to the action of pathogenic secretions from the damaged mantle.

There are several parasites of *Mytilus edulis.* The Annelid worm, *Polydora ciliata,* enters through a hole the size of a pin and makes a U-shaped burrow in the shell. It is usually harmless in that it does not attack the soft tissues of the mollusc, but if it is large it may cause the mussel to form a pearly excrescence. Frequently the worm gets into the shell opposite to the posterior adductor muscle and the resulting lump in the shell destroys the muscle. *P. ciliata* is a common parasite in oysters, where it is larger than in the mussel, and it is therefore more abundant in mussels which inhabit areas close to oyster beds.

Field described a new parasite which he called *Haplosporidium mytilovum.* This is a Sporozoan which inhabits the egg. Field says "its presence [in the egg] there gives rise to a phenomenon suggesting the formation of a chromatin vesicle which for a long time the author took to be a normal process in the development of the egg." The Sporozoan creeps by amœboid movement within the follicles and genital canal. Inside the egg, or even within its nucleus it forms a multinucleate cyst which gives rise to uninucleate spores.

Trematode larvæ occur in the mantle, foot and liver of *Mytilus edulis.* The cercariæ encysted in the liver are called by Jameson *Distomum* (*Gymnophallus*) *somateriæ* and by Odhner *G. bursicola.* The cercaria of *Echinostianum secundum* encysts in the foot and Lebour believes she has found the previous stage of this in *Littorina littorea* at Budle. Two per cent. of the specimens examined had the liver full of orange-coloured rediæ containing tailed cercariæ which agree with the encysted form. There is a third type of cercaria found in the liver which has not been determined. Nicoll suggests that, though not connected with the cercaria of the foot, it may be a stage of the species found in the mantle. Nicoll has discovered the mature phase of a similar Trematode, which occurs in *Cardium* (*Cerastoderma*) *edule,* in the lower part of the intestine of the oyster-catcher, *Hæmotopus ostralegus.* Jameson suggests that the sporocysts of *G. somatoriæ* are in *Paphia* (*Ruditapes*) *decussata* and *Cardium* (*Cerastoderma*) *edule,* and that the Vertebrate host is the black duck, *Œdemia nigra.* There is no evidence that these Trematodes injure the molluscs containing them.

Pearls are formed within the mantle of *Mytilus edulis.* They are quite common in specimens from enclosed or brackish water, but are very small in size. Jameson describes seven theories which attempt to account for the presence of pearls in some bivalve molluscs. These theories suggest that pearls are concretions of shell-forming fluid ; shell substance which has been deposited around bodies or concretions of internal origin ; formations round an aborted or misplaced ovum ; secretions to coat over a grain of sand; the result of an injury or perforation of the shell; result of the presence of a parasite; or formations in an ampulla in the tissues. Jameson believes that pearls in *Mytilus edulis* are formed round the encysted cercariæ of *Gymnophallus somateriæ*, and that they consist of layers of shell substance enclosing a central nucleus. They are formed in a sac which is embedded in the tissues and has itself been laid down around the parasite. Pearls have been shown in other molluscs to be due to an abnormal behaviour of the shell glands of the mantle, and it will probably be found to be the same in *Mytilus edulis*. The hardness of the pearl and consequent difficulty in investigating the structure of its centre is mainly responsible for the differences of opinion as to the nature and formation of pearls.

ECONOMIC IMPORTANCE.

The shells of the tropical members of the Mytilidæ are of commercial value in that they give the jeweller the "Oriental pearl." They are also employed in the formation of various articles of differing degrees of value and ornamentation. The byssus, too, may be so large in these forms that its fibres are used for the formation of a cloth in places where clothing materials are scarce. *Mytilus edulis* forms small pearls which were once of commercial value, but the industry has now died out. The mussel is used in most countries where it occurs, both for bait and for human consumption, but the premium put upon its value varies. As far as human consumption is concerned, France stands the highest of any country, and mytiliculture is a flourishing industry. The demand is even greater than the supply, and quantities are imported, chiefly from Holland and Belgium. Mussels are also eaten in Spain and Portugal, and to some extent in Germany, Norway and Great Britain. Field (1921–22) says: "they are now beginning to be appreciated as a wholesome food in this country" [United States]. *Mytilus edulis* is highly important as bait, especially in Europe, but less so in America. Crushed mussels are also thrown overboard by mackerel fishers to attract their fish. Mud taken from old mussel beds is organically very rich, and makes a valuable manure which is specially suitable for carrots and onions. The shell is variously used. It is employed by oyster cultivators to catch their spat, and it is carved and polished to form various ornamental articles.

In Great Britain mussels are collected by raking, hand-picking and dredging in most areas where they occur, from September to April, with an extension to May in some parts of the east coast. The summer period is the "closed" season for Mytilus. Figures taken from a Fishery Report for 1911 indicate the state of the industry before the war. These do not give mussels separately but quote the number of shell fish other than crabs, lobsters and oysters, and in this category *Mytilus edulis* would be the most important, the other species—*Cardium* (*Cerastoderma*) *edule*, for instance—being of only local value. These figures show that 447,105 cwt. valued at £111,770 were landed, while some 110,000 cwt. were imported, mainly from the Netherlands. In the same year 10,419 cwt. were exported to Belgium, 13,762 cwt. to France and about 3,000 cwt. elsewhere.

Since the war the German consumption has increased to a great extent, and a flourishing industry has arisen in Holland to cope with the demand.

Food Value.

The total food value of the mussel exceeds that of the lobster and the oyster, its carbohydrate content being the largest among shellfish, but the proteid and fat content are less than that of the lobster.

Extracts from a percentage composition table drawn up by Daniel in 1922 and calculated from Morecambe Bay specimens are interesting:

	Water.	Dried flesh.	Proteid.	Oil.	Ash.	Carbo-hydrate by difference.	Glycogen.
Sept. .	80·1	19·9	9·8	1·3	1·7	7·1	2·5
Dec. .	81·4	18·6	10·2	1·5	1·9	5·0	2·7
April .	83·2	16·8	9·8	1·3	3·8	1·9	1·0

The figures for April are taken from individuals which have finished spawning, and the mussel is therefore no longer "fat," the degree of fatness in mussels being dependent on the amount and condition of the sexual organs.

Glycogen occurs in practically all the tissues of the body, except in the digestive gland and in the epithelium of the gut. Neither MacMunn nor Daniel could find any traces of it in the digestive gland.

The fat content is small, as it is in all shellfish. The quantity, such as it is, shows a steady increase until the time of spawning, when it drops. Daniel found it in the lining epithelium of the gut and in the digestive gland, where it is relatively greater than in the other tissues and where it does not seem to vary with the condition of the genital organs. Fat accumulates in the connective tissues round the genital products, and it is here that the rise in the fat percentage which is apparent before spawning is localised.

The proteid content was found by Daniel to rise throughout the season from one spawning to the next, with a slight depression about February.

Daniel observes that the mussels, even when deprived of food, do not draw upon these reserves, which are stored up for the gonads.

Mussel Poisoning.

There are two clearly separated forms of mussel poisoning. The minor form which is called "musselling," where the individual suffering from it is said to have been "musselled," is in no way due to the condition of the mollusc. The illness, which is always characterised by the presence of a red rash, is a personal idiosyncrasy and is comparable with the effect that the consumption of strawberries or eggs or the sight of a cat has on some people.

The serious form, which is frequently fatal, is due to a toxin within the animal. The characteristic symptom is that of paralysis, and death, if it occurs, is due to respiratory paralysis. The resultant illness is, therefore, similar to strychnine poisoning. The poison is an alkaloid one, which according to Brieger, is trimethylglycerammonium hydrate, or mytilotoxine. It is probably a derivative of betaine. Brieger found considerable quantities of this substance in mussels, and suggested that it was derived from the glycogen of the muscles. This disease is brought about by the consumption of unhealthy mussels. Popular ideas as to the locus of mussel poisoning favour the byssus, the foot and the crab *Pinnotheres pisum,* which is sometimes found in the mantle cavity. As the crab, however, lives only in healthy mussels, this suggestion is even more erroneous than popular ideas usually are. Naturally the byssus would be unpalatable and indigestible, but the foot is no more dangerous for consumption than is any other part of a healthy mussel.

Arsenic in small quantities is present in mussels as in most organisms, but Dodgson has calculated that it would be necessary to consume 1½ to 2 quarts of mussels in order to take one grain of arsenious oxide. Varying amounts of copper are also present in mussels, but Dodgson says there is no evidence that it is in harmful quantity.

Mussels are certainly a means for the distribution of typhoid fever. They are ciliary feeders, and are, of course, very liable to sewage contamination. Mussel beds are close to the shore and are frequently near to sewage outfalls, and therefore there is every likelihood that the molluscs will take in the germs of bacterial infection.

I am indebted to H. A. Cole of the Fisheries Experiment Station, Conway, for the following: "Attempts to grapple with the gross and constantly increasing sewage pollution of shellfish beds, and the liability to the spreading of gastro-intestinal diseases by the consumption of mussels, have been made; but the measures adopted have generally been ineffective. Since the year 1915, however, the Ministry of Agriculture and Fisheries has been operating, with complete success, a system of mussel cleansing in tanks. The process is, briefly, as follows: The mussels are spread on wooden grids in shallow tanks (each of which is capable of dealing with 6 tons of shellfish at one time) and thoroughly hosed with high pressure water to remove adherent mud, etc. Water sterilised with 3 parts per million available chlorine (but from which all residual traces of chlorine, after sterilisation of the water, have been removed by sodium thiosulphate [hypo]) is then run on to the mussels. In this bath of sterilised, chlorine-free water, the mussels remain for twenty-four hours, and into it they discharge all foreign matter, including bacteria, from their intestines, mantle cavities, etc., in the form of fine threads and small pellets (fæces and pseudo-fæces) held together by mucus. These fall to the bottom of the tank, the bacteria discharged with them remaining imprisoned in the tenacious and practically insoluble mucus. After twenty-four hours the water is drained off and the mussels are again hosed, the matter discharged by the mussels being washed through the grids and flushed away. The mussels are then subjected to a second bath, of twenty-four hours' duration, of sterile water; and the hosing is again repeated. Finally, for the purpose of sterilising the outsides of the shells, the mussels are given a bath of water containing 2 parts per million active chlorine. In this bath, owing to their inability to tolerate the presence of chlorine, the mussels remain tightly closed. After one hour this bath is drained off, and the fishermen pack the mussels into sterilised bags, which are sealed with the Ministry's dated lead seal and despatched to market. A small charge is made to the fishermen for each bag of mussels so treated, and it is obvious that mussels from bags bearing the Ministry of Agriculture and Fisheries' lead seal should fetch a better price in the market than those which have not undergone the treatment. A similar installation has, for the past two years, been operated by the Lancashire County Council, under the supervision of the Ministry of Agriculture and Fisheries, at Lytham."

Public Health (Shellfish) Regulations, 1934, requires that the Medical Officer of Health shall investigate and report to the Local Authority any suspected mussel beds. The Local Authority then has powers to prohibit the sale of mussels from any bed, or else to order satisfactory and approved cleansing processes. These regulations can be considered as encouraging the good conduct of the industry.

There are many recipes available for cooking mussels. The mussels are not killed first, but are washed and then placed in a stew pan and heated until they open. Owing to the mollusc's habit of retaining sea water within the tightly closed shell, it is not necessary to use much water in the pan. It is suggested that the purity of the mussels can be tested by putting a silver spoon into the liquid resulting from the stewing. If the spoon blackens the whole should be thrown away. A book of recipes written by the cooks of King Richard II (1390) gives a method for " Muskels " in broth.

FOSSIL RECORD.

The family Mytilidæ occurs as fossils from the Devonian to the present day, the earliest recorded genus being the Devonian *Modiolus*. The genus *Mytilus* is first found in the Lower Triassic. Zittel describes *Mytilus* Linné as follows : " Shell elongated, thin, with terminal pointed beaks ; valves wider and rounded behind, gaping a little at the byssus, smooth or radially sculptured, with smooth margins, conspicuous epidermis, and a thin nacreous layer ; hinge with a few small teeth under the beaks, or edentulous."

Mytilus edulis occurs first in Europe in the Upper Pliocene (Red and Norwich Crags) of East Anglia, where it may be very abundant in places. The specimens are reported to be very thin and fragile. Wood gives the specific characters as follows : " Shell elongate, of a subtrigonal form, smooth, anterior part curved, subangulated, posterior obtuse, tumid towards the base, hinge with three or four denticles." The greatest diameter is 4 inches. Wood records these localities : Red Crag : Sutton, Bawdsey, and Ipswich ; Mammaliferous Crag : Bramerton and Bridlington ; Recent : Mediterranean, Britain, Scandinavia and North America. Wood figures five varieties—*elegans*, *antiquorum*, *incurvatus*, *saxatilis* and *alæformis*. In addition to the above-named Recent records, *Mytilus edulis* has been found in the Pleistocene of Canada and Alaska. U. S. Grant and H. R. Gale state that " the earliest occurrence of *Mytilus edulis* on the Pacific coast may be in the Lower Miocene, where it is represented by *M. sammishensis* and *M. snohomishensis* Weaver, two Blakeley formation species which are either conspecific with *edulis* or its ancestor."

EXTERNAL CHARACTERS.

A. **The Shell.** (Figs. 1, 2, 3, 28, 29.)

The Lamellibranchiata are characterised by the presence of a double or bivalve shell which is secreted by the two lobes of the mantle. In the majority of cases the shell is capable of covering and enclosing the whole animal when it is in the retracted condition and thus forming a *closed* shell. *Gaping* shells, on the other hand, are those which by reason of their shape or limited size are unable to enclose the animal entirely.

Primitively the shell is the same size and shape in the two halves. In more highly evolved forms it may still be equivalve in this way, or it may become asymmetrical. In all Lamellibranchs, with only a few exceptions, the two valves fit close together along the dorsal side, the ventral, anterior and posterior borders being capable of separation. Articulation between the right and left halves is brought about through the presence of interlocking teeth. These occur in varying degrees of development, and when prominent prevent any antero-posterior movement in allowing the shell to open only laterally. A ligament is also present on the mid-dorsal line which may be either completely internal or external or partially so. Its function is opposed to that of the adductor or closing muscles of the shell and by its elasticity brings about the opening of the shell.

The umbo or apex of the valve is situated dorsally and has beaks which generally point anteriorly. It lies in front of the ligament. The portions of the shell anterior and posterior to the umbones may differ in size, when the shell is referred to as "inequilateral," or they may be exactly the same size and shape, when the shell is "equilateral."

Beneath the umbo, internally, lies the lunule. This is an area consisting of alternating ridges and furrows which travel across from the teeth to the umbo. The teeth themselves are continuous with the furrows, and the hollows between the teeth are continued upwards as the ridges.

The larval portion of the shell, the prodissoconch, is often distinctly marked off from the rest of the shell, possibly by a well-marked ridge.

The Lamellibranch shell is composed of three layers. The outer layer, the periostracum, is horny and is a thin layer which is frequently worn off in older shells. The periostracum is secreted by part of the margin of the mantle. The middle, or prismatic layer is composed of prisms of carbonate of lime embedded in an organic matrix ; this also is secreted by part of the mantle edge. The inner, nacreous or pearly layer is laminated in structure and calcareous ; this layer is secreted by the whole of the external surface of the mantle.

The ligament is usually of two layers, of which the outer, non-calcareous, inelastic one is continuous with the periostracum of the shell. The inner ligament layer, which is usually sub-divided, is elastic and calcareous. Where the ligament is internal it fits into a series of small depressions which lie along the hinge area posterior to the hinge teeth.

Within the shell are to be found impressions or scars where the muscles were attached in the living animal. These impressions are most marked in the case of the anterior and posterior adductor, or closing muscles of the shell, or of the posterior only. Where there are two adductor muscles we have the Dimyarian condition, and when only one the Monomyarian. There are also the scars of the pallial muscles which leave an impression parallel with the edge of the shell, called the pallial line. In those forms which have siphons developed from the mantle edge there is a large indentation posteriorly, called the pallial siphon. In addition there may be the impressions of various muscles which control movements of the foot, and of the byssus when present.

The shell of *Mytilus edulis* is somewhat heavy. It is equivalve and markedly inequilateral. The general shape is that of an elongated triangle, but there is a good deal of variation in the form, which is, of course, due to the mode of life; *Mytilus edulis* being highly gregarious, the consequent overcrowding prevents free development of any one particular animal.

The size of the adult mussel varies from 2 to 4 inches in length, 1 to 2 inches in depth and $\frac{3}{4}$ to 2 inches in breadth; young specimens are proportionately narrower.

The posterior border of the shell is nearly a semi-circle which becomes flattened towards the dorsal side, where a nearly straight line passes up to the hinge. The hinge extends down from an angle of about 45° as a straight or slightly convex line to the extreme anterior end, which is pointed. The ventral border is nearly straight with a slight tendency to concavity. This tendency is increased in specimens which have come from exposed situations. On the other hand, specimens from piles and very protected areas have a somewhat convex ventral line.

The umbones (fig. 1, U.) are completely terminal, thus showing the extreme condition of inequilaterality. The position of the umbones differentiates *Mytilus* from the closely allied genus *Modiolus* (the horse mussel), where the umbones are not terminal.

The ligament (fig. 1, L.) is dark brown, elastic, and is situated internally. It lies in a groove in each valve. The walls of the groove, the ligament ridge (fig. 1, L.R.), have a characteristic structure, being very white in colour and perforated by strongly marked pores. The ligament unites the two valves together and is strongly compressed when the shell is closed. To shut the shell the animal contracts the posterior adductor muscles with great force. These muscles naturally relax when the mussel is dead or dying and the elasticity of the ligament then forces the valves apart. This accounts for the opening of dead or unhealthy specimens. A recently dead mussel usually "gapes" in this way, though one that has been dead and out of water for some time will close up again. This is due to the ligament drying up and losing its elasticity and therefore not forcing the valves apart.

The two valves of a normal specimen with the periostracum intact fit very closely together, so that when the shell is closed there are no places where the edges do not meet, consequently sea water can be retained within the pallial cavity. (See below, **Mantle.**) This fact helps to account for the occurrence of *M. edulis* as a littoral species, and it is useful economically as it facilitates keeping supplies in a living and fresh condition for a fair period of time. (See HABITAT.)

The hinge area (figs. 2, 3, H.) lies below the umbo. The teeth (H.T.) are covered by the periostracum, which is continuous dorsally from one valve to the other, and are so arranged that the teeth of one valve fit into sockets in the other. The teeth are variable in size and number, from one to six having been found, with three or four as the commonest number. These structures are better considered therefore as denticulations than as true hinge teeth, which are a specific constant.

The lunule (figs. 1, 2, 3, LU.) stretches from the denticulations to the umbo. It is composed of furrows corresponding with the teeth, and of ridges corresponding with the depressions between the teeth.

The periostracum (fig. 29, PER.) or outer horny layer is glossy, dark blue when wet and brown when dry. It is thin and translucent so that it is in part responsible for the characteristic variations in the colour of the shell during life.

The prismatic layer (figs. 1, 29, PR.) contains dark blue pigment. This pigment is arranged in bands of varying number which radiate from the umbo. When the bands are very frequent and close together the shell is dark blue, but in the absence of the pigment it is a yellowish white, and is darkened in life by the periostracum. To find the natural colour of the prismatic layer the shell should be soaked in strong caustic soda or potash and it will then be possible to remove the periostracum with a brush.

The inner layer of the shell is the nacreous layer (figs. 1, 29, N.), and the inner surface of the shell shows a well-defined line which commences posterior to the hinge, passes along the dorsal surface posteriorly, and is continuous forward as far as the anterior part of the shell. Outside this line the nacreous layer is not present and the shell is deep blue, owing to the middle layer being seen. The nacreous layer is pearly white with a green, blue or pink tinge. The position of the line separating the inner and middle layers of the shell corresponds with the position of the outer fold of the mantle. (See below.)

Except for the concentric lines of growth the shell is smooth, and there are no ridges or tubercles which are frequently present in Lamellibranch shells. The growth lines are, however, strongly marked, especially in those specimens which have been removed from an unfavourable to a favourable habitat. The sudden increase of growth can be clearly seen.

After treatment with caustic soda or potash it will be seen that there is a region on the mid-ventral line where the valves do not meet. This is covered during life by the periostracum and is the place where the byssus emerges.

There are six impressions on the inside of the shell which are caused by the insertion of the muscles. These are dark blue in colour (fig. 1).

1. The pallial line (P.L.) is the impression of the retractor muscles of the mantle edge. It is a continuous line which runs $\frac{2}{5}$ to $\frac{4}{5}$ of an inch from the edge parallel with the shell margin, from the posterior end of

the ligament round the posterior side of the shell and ventrally to the anterior adductor scar. On the postero-ventral and ventral surfaces it has an indented outline. Behind and below the scar of the posterior adductor muscle there is a large indentation which corresponds with the rudimentary pallial siphon.

2. The posterior adductor scar (P.A.S.) is the largest single muscle impression. It is clearly defined and more or less circular in outline; it lies somewhat dorsally and about $\frac{1}{3}$ of the length of the shell from its posterior border.

3. The anterior adductor scar (A.A.S.) is a small irregular impression lying under the anterior extremity of the hinge.

Between the posterior termination of the ligament and the scar of the posterior adductor muscle there is a series of somewhat irregular scars parallel with the dorsal margin of the shell. The anterior of these is the impression of

4. The retractor muscles of the foot (R.P.S.), while the posterior ones are those of

5. The posterior byssal retractor muscles (P.B.R.S.).

6. The anterior byssal retractor muscle scar (A.B.R.S.) is dorsally placed under the ligament. It is small and bilobed, but clearly defined.

MICROSCOPIC STRUCTURE OF THE SHELL.

[The shell should be broken across. This is easily done with the hands, and the section if examined with a lens shows the three layers.]

The periostracum appears as a thin yellow-brown cuticle. The middle prismatic layer is deep blue. The prisms of the latter are long and are arranged obliquely across the shell, forming an angle of about 45° with its outer surface. The pigment is deeper on the outside and lies across the prisms in parallel lines. These prisms are embedded in an organic matrix.

The nacreous layer is white. It is thickest in the middle and anterior regions, especially in the latter, and thins out ventrally and posteriorly where it does not meet the edge of the shell. The result of this is that round the ventral and posterior border of the shell the mantle is in contact with the prismatic layer. The nacreous layer consists of thin lamellæ which lie parallel with the surface of the shell. The nacreous is the only layer which continues growth in thickness throughout the life of the animal.

A section cut across the ligament will show that it is composed of three layers, the outer of which is the periostracum, the middle a pale brown homogeneous layer, and the inner similar, but with dark brown bands.

[The shell may also be examined microscopically, and to do this it is necessary to mount a thin section on a slide. This is not easy to do owing to the brittle nature of the shell. The method is that used for petrological work. A strip of the shell should be cut with a fret-saw to about ¼ of an inch thick. The strip is then ground on a carborundum wheel or plate until it is too thin to hold in the hand. It is then fixed with pure hot Canada balsam. Care must be taken that the Canada balsam is not under-heated or the section will slide off the glass, and if over-heated the Canada balsam will flake off. Canada balsam is "cooked" correctly when a thread of it drawn out between two needles will snap sharply. The section is then ground again until it is as thin as possible. After this the slide is washed in soapy water, thoroughly dried, mounted in Canada balsam dissolved in xylol, and covered with a cover slip.]

Under the microscope the periostracum shows three layers, of which the outer and inner are clear yellowish brown, while the middle one is colourless, vacuolated and can be stained.

The prismatic layer does not show more than has been seen under a lens.

The lamellæ of the nacreous layer now appear as irregular fine parallel lines, this layer being composed of flat sheets, unevenly rectangular, and with a zigzag edge. The transverse plane of cleavage follows these edges.

The ligament now shows four layers; the outer periostracum is typical but the middle layer consists of an outer homogeneous layer which is yellow, and may be stained blue or green, and an inner darker layer containing crystals of calcium carbonate which give it a granular appearance. The innermost layer consists of fine lines travelling at right angles to the surface with the dark bands running across them.

FORMATION OF THE SHELL. (See below, **Mantle.**)

COMPOSITION OF THE SHELL.

The shell consists of an organic base with mineral salts. The base, which gives the shell its tough unyielding structure, is an albuminoid, conchiolin. Field quotes Wetzel in giving the composition of conchiolin as Carbon 52·3 per cent., Hydrogen 7·6 per cent., Nitrogen 16·4 per cent., and Sulphur 0·65 per cent. This substance forms the periostracum and the matrix of the prismatic layer.

The inorganic matter is mainly calcium carbonate with some other minerals. Field gives the following analysis of Adrian Thomas.

	Per cent.
Calcium Oxide	51·21
Magnesium Oxide	0·27
Iron and Manganese Oxides	0·32
Silica	0·11
Carbonates	37·33
Sulphates	1·02
Organic	8·05
Water	0·58
Phosphates, Chlorides, and Sulphides	Traces

B. **The Mantle**. (Figs. 4, 5, 9, 10, 11, 14, 16, 19, 26, 28, 29, 30.)

[*To open the shell insert a blunt scalpel between the two valves and then gently press them apart until it is possible to turn the scalpel on edge, thus using it as a wedge. Then put a sharp scalpel through the opening between the valves and cut the posterior adductor muscle away from one valve. Do this as close to the shell as possible, and the shell will now gape. Next with the scissors cut along the ventral side through the periostracum which will be found to extend from the shell to the mantle. Next scrape along the pallial line with a scalpel so as to separate the pallial muscles from the shell. Do this ventrally first, and then along the posterior border and finally dorsally. Now cut along the ligament with scissors, after which the pedal and byssal muscles should be separated from the shell. Finally the anterior adductor and anterior byssal muscles should be very carefully cut. One valve can then be lifted off and the animal left lying in the other, from which it should not be removed until all the external features have been examined previous to dissection.* Mytilus edulis *contracts very much when entirely removed from its shell.*]

The mantle of the Lamellibranchs consists of two thin lobes which are attached to one another and to the visceral mass dorsally, and then extend down each side of the body as far as the ventral surface. Through the separated lobes water with food matter and dissolved oxygen enters, and also leaves with the waste products of respiration, digestion and excretion. The reproductive elements escape in the same way.

A completely open mantle is found in the primitive genera, but the more usual occurrence is the presence of thickenings of part of the mantle edge which cause concrescence of some part or parts of the ventral surface. There are many different forms of mantle resulting from these one or more points of fusion, which separate a dorsal exhalent aperture from a ventral inhalent one. These apertures frequently have their edges drawn out to form a more or less elongated tube, which is termed the exhalent or dorsal and the inhalent or ventral siphon.

Differentiation of the mantle edges also occurs to form protuberances and papillæ, tentacles, eyes and glands.

Typically the mantle is rather thin with an external and an internal epithelium enclosing some connective tissue and muscle fibres. The gonad in the Anomiidæ extends into the right lobe, and in the Mytilidæ into both lobes, and when this is the case the lobes are increased in thickness up to 100 times the original diameter.

The mantle margins are usually separated into folds which are typically three in number. Specialised parts of the mantle folds secrete the shell, the outer periostracum originating in the outer surface of the middle fold, the middle prismatic and the inner nacreous in the outer surface of the outer fold of the mantle. Growth in thickness of the nacreous layer is provided for by the whole of the outer surface of the mantle.

In *Mytilus edulis* the mantle is united along the mid-dorsal and anterior surfaces from the region above the anterior adductor muscle as far as the anterior edge of the posterior adductor muscle. Between the dorsal face of the visceral mass and the united mantle edges a cavity, the so-called cavity of the flanks (figs. 26, 29, C.F.) is formed. Posteriorly the free edges of the mantle are united by a triangular-shaped band of muscle and connective tissue, the branchial membrane (fig. 14, BR.M.). Between the branchial membrane and the dorsal union of the mantle an aperture is formed about $\frac{3}{8}$ inch long in a 3-inch specimen. This is the exhalent aperture (fig. 14, EX.AP.) and as there is no other point of concrescence there is no defined inhalent aperture. The inhalent water current, however, enters the pallial cavity just below the branchial membrane.

The mantle is normally of a creamy colour except on the postero-ventral edge, but during the period of sexual activity the colour is increased, especially in the female, where it may be a deep reddish orange.

A broad band of muscles, the pallial muscles (fig. 4, PL.M.), encircle the free part of the mantle. The fibres travel at right angles to the mantle border and are inserted into the shell about ¼ inch from the mantle edge. These muscles are white. There is a widening of the muscle band posterior to the posterior adductor muscle. This is the rudiment of the siphonal muscle, which is well developed in those forms which have a siphon.

The mantle edge in *Mytilus edulis* is divided into the three typical folds (figs. 26, 28, 29, 30). The outer fold of the mantle is the thinnest of the three (MANT.O.) but it contains the pallial muscles. In the living condition it cannot be seen, as the periostracum of the shell, attached to the middle fold, completely encloses it. It is therefore bounded on its outer surface by the shell and on its inner by the periostracum, and it is not exposed to the outer world at all. This outer layer secretes the the prismatic layer of the shell through low columnar epithelial cells, and the nacreous layer by small glandular cells.

The middle fold (MANT.M.) is thinner than the inner but thicker than the outer mantle fold. Its inner surface is lined with a ciliated epithelium, and some brown pigment is also present on the surface in the posterior region. The periostracum is secreted by long epithelial cells which lie obliquely to the surface.

The inner fold (MANT.I.) is very thick. Anteriorly its edge is smooth, but towards the ventral border it becomes fringed, and as the posterior edge is reached the processes thus formed become larger and subdivided. Its outer ciliated epithelium is dark brown posteriorly, due to the presence of brown pigment granules. This inner layer is richly supplied with muscle fibres which render the inner and middle folds highly contractile. Under water, with the shell open, this part of the mantle is frequently thrust well out of the shell. It is, however, very sensitive to stimulation, and retracts at once on being touched or subjected to change of light intensity. This retraction of the mantle and closing of the shell is brought about very rapidly.

The outer epithelium of the mantle adheres to the shell through the presence of patches of glandular adhesive cells which are scattered over its surface. The pallial muscles arise in the mantle and are inserted into the shell and the periostracum bends round from the middle fold (see fig. 29) ; these are the only direct connections between the adult shell and the mantle. Although the outer fold secretes the middle layer of the shell entirely, and the inner layer of the shell in part, it is not united with it at the edges.

The branchial membrane (fig. 14, BR.M.), which is situated posteriorly and unites the two halves of the mantle, is a triangular flap with a small lobe on its mid-ventral edge. It is connected at the sides with the inner mantle fold. It is composed of connective tissue and muscle fibres, and is capable of expanding and contracting, which brings about the raising and lowering of the whole structure. The raising and lowering of the branchial membrane is compared by Dodgson with the raising or lowering of a blind. Its outer surface is covered with a ciliated epithelium with contained pigment granules.

Two other flaps of thinner tissue are present across the exhalent aperture. The dorsal one is triangular in shape and is attached dorsally and laterally to the inner mantle fold ; it reaches two-thirds of the way across the exhalent aperture. The ventral one is oblong and is attached by its lower border to the dorsal part of the branchial membrane. These two flaps are the dorsal or anterior velum (D.F.) and the ventral or posterior velum (V.F.).

Part of the nervous, vascular, reproductive and muscular systems of the mussel are to be found in the mantle. These can be made out more or less easily and should be investigated before any dissection is attempted.

The pallial nerves can be seen in preserved specimens, and in fresh ones after a little alcohol has been poured on the mantle. They lie on the outer surface of the mantle (fig. 10).

The genital canals can also be seen externally. They appear as granular inflated lobes and ducts which stand out as ridges in both immature and mature specimens, but show most readily when the mantle is not too congested with genital products (fig. 10).

The pallial arteries are also external and can easily be seen as clear lines in a fully mature mantle. In a thin mantle they are not so easy to make out, as they are not so clearly differentiated from the surrounding tissues (fig. 19).

The pallial veins are on the inner surface of the mantle and are difficult to see.

The following muscles pass through the mantle lobes to their insertion on the shell (figs. 1 and 4). The large posteriorly situated muscle which unites the two halves of the shell is the posterior adductor muscle. The other unpaired muscle is the small anterior adductor muscle, while there are the paired anterior byssal retractor muscles, the paired pedal retractor muscles and the paired series of posterior byssal retractor muscles. One of each of the paired muscles passes through the mantle lobe of its side, while the anterior and posterior adductor muscles pass right through the animal from one valve of the shell to the other. Further details as to the position of these muscles have been given under **The Shell**.

The space formed between the overhanging mantle lobes is named the pallial cavity (PAL.C.). Dorsally this is bounded by the visceral mass. (For details of pallial cavity see fig. 5.) From the visceral mass posteriorly there is suspended a fold of the body wall termed the mesosoma or "abdomen" (MES.), which in a mature specimen becomes very much distended with the ramifications of the gonads. In addition, the pallial cavity contains anteriorly the paired outer and inner labial palps (fig. 5, O.L.P. and I.L.P.). These are pale pink, smooth and soft and are capable of a considerable amount of contraction and expansion. When expanded, the labial palps are long triangular flaps. The outer palps unite to constitute the dorsal lip of the mouth, while the inner ones form in the same way the ventral lip.

The gills (fig. 5) are a double row of reflexed filaments hanging from the ventral side of the body on each side of the visceral mass. They are white, but may be pigmented at the edge where the descending part or lamella turns up to form the ascending lamella.

The foot (F.) and byssal apparatus (B.A., and fig. 4, B.) are median in attachment, and occupy approximately the middle of the pallial cavity along the antero-posterior line. They are described in detail below.

There are two median and two paired apertures opening into the pallial cavity.

The mouth (fig. 9, M.) is a mesially placed slit bounded by the dorsal and ventral lips; the anus (fig. 9, AN.) opens into the pallial cavity on the posterior surface of the posterior adductor muscle. Hence, it is very close to the exhalent aperture.

The paired genital (fig. 5, GON.A.) and excretory (E.A.) apertures open into the pallial cavity on a papilla which is situated mesial to the gill axis anterior to the posterior adductor muscle. It is quite conspicuous and of a white or pale pink colour; the excretory aperture is separate from and lies behind and just below the genital opening.

Before terminating the examination of the pallial cavity, the student should find the cerebral and visceral ganglia and their commissures. The ganglia are yellow or orange in colour and can be seen through the integument. The cerebral ganglion (fig. 30, C.G.) lies in the angle where the inner labial palp passes into the ventral lip. The combined cerebro-visceral and cerebro-pedal connective can be seen leaving it and passing across the anterior byssal retractor muscle. The visceral ganglia (V.G.) lie mesial to the gills on the antero-ventral side of the posterior adductor muscle. The cerebro-visceral connective can be seen for a great part of its length lying mesial to the gills.

C. **The Foot.** (Figs. 4, 5, 9, 18, 28, 30.)

The foot, which is a muscular development of part of the ventral region of the body, is a characteristic structure in the Mollusca. In the Lamellibranchiata, as in the other groups, the foot both in size and shape is modified in relation to the habits of the species. It is composed entirely of muscular tissue, though it may be invaded by parts of the viscera, such as the digestive diverticulum, one of the coils of the gut, or even on its outer surface by the gonad. It has its own vascular and nervous tissue but no connective tissue. The muscles of the foot are normally four pairs, which originate in the foot and form its substance. They are inserted into the right and left valves of the shell between the anterior and posterior adductor muscles. These foot muscles are primitively a pair of anterior protractors and retractors, a pair of median elevators and a pair of posterior retractors. This is the condition in simple forms and in some Protobranchia, while in more complex genera only the anterior and posterior retractors are present. In other genera, where locomotion is reduced and a well-developed byssus is present, the posterior pedal muscles originate from the byssal apparatus and not from the foot. (See below.) In these cases the foot is a direct continuation of its retractor muscle and has no further connection with the elevators and protractors.

The **foot** (fig. 5, F.) of *Mytilus edulis* is an elongated tongue-shaped structure; it is the "tongue" of the fishermen. On its posterior side it has a deep groove which extends the whole of its length, commences proximally at the aperture of the byssus (fig. 5, B.A.), and terminates distally in a rounded depression (F.S.). This depression is used as a sucker by means of which the animal can adhere to a solid structure. The groove has somewhat crenate edges even when the foot is expanded, but when it is contracted the crenations become deeper, and the line of the groove itself becomes sinuous.

The main bulk of the foot (see fig. 28) is made up of longitudinal muscle fibres which are direct continuations of the paired pedal retractor muscles (R.P.). These are the only extrinsic muscles of the foot of the adult mussel. Superficial to these longitudinal fibres is a very thin band of circular muscle fibres, while at the tip of the foot there are some oblique fibres. The foot is covered by a ciliated epithelium which frequently has a well-developed brown pigmentation.

Between the right and left bands of muscle fibres there runs an extension of the byssus gland.

D. **The Byssus.** (Figs. 4, 5, 18, 26 and 28.)

The Lamellibranch byssus organ consists of a byssogenous cavity or pit which leads through a duct to the exterior, where the duct opens out as the byssus aperture. The byssus aperture is continuous with a groove along the foot. Its walls are surrounded by parts of the byssus muscles and the byssus glands. These glands primarily surround the byssogenous cavity, lying between the byssus muscle, and extend down the foot between the right and left pedal retractor muscles.

The byssus organ is not much developed in the Protobranchia, where there is no functional byssus, but it is functional in various Filibranchs and Eulamellibranchs. When at its maximum state of development, the byssogenous cavity contains a number of lamellæ or folds, and the trunk of the byssus is thick, owing to the union of many threads of conchiolin, and there is a groove in the posterior side of the foot running from the byssal aperture to the apex of the foot. This groove contains many unicellular glands.

This maximum development of the byssus occurs in *Mytilus edulis*. It may be described under four heads.

(1) The muscles of the byssus. (For a description of these, see MUSCULAR SYSTEM.)

There is a paired anterior byssus retractor muscle (fig. 4, A.B.R.) and a series of paired posterior byssus retractor muscles (P.B.R.), all of which originate behind the foot and are inserted into the shell.

(2) The byssogenous cavity or pit and the byssus glands.

These have been worked out by Boutan, Tullberg, Williamson and others.

The byssus cavity lies between the points of origin of the byssus muscles. It is roughly the shape of an inverted pear, with the body of the pear forming the cavity and the narrowed stalk portion forming the neck of the byssus organ, which is formed of pedal and not byssal muscles. The byssogenous cavity (BY.C.) is divided into a great number of small slit-like compartments by the lamellæ or septa (see fig. 28). Each septum is formed of connective tissue, muscle fibres and unicellular glands. The muscle fibres are derived from the byssal muscles, each septum being in connection with a complete series of byssus muscles. The septum is coated with a gelatinous layer and ends in a clear lip.

The byssus glands (B.G.) are divisible into two groups—those of the foot and those of the byssus cavity. The foot has a major and a minor gland. The former is white, and is hence named the white gland. It extends through the whole length of the foot on the three sides of the byssus groove, and when seen through the tissues of the foot appears yellow. The minor gland, the so-called purple gland, overlies the white gland. Towards the apex of the foot it becomes larger than the white gland. The purple gland discharges its secretion into the sucker at the free end of the foot (fig. 5, F.S.). Surrounding the byssus cavity are prolongations of the white gland. In addition to this there are the above-named unicellular glands of the lamellæ, and these two form the gland of the byssus cavity.

(3) The byssus. (Fig. 4, B.)

The byssus itself arises as thin sheets of transparent material which lie between the septa. Tullberg and Boutan assert that these sheets are formed from the lamellæ, but Williamson states that they are secreted by glands of the byssus cavity. The thin sheets are moulded together as they pass through the byssogenous cavity and the neck of the cavity, and when they traverse the aperture of the latter they do so as a solid rod, the byssus stem or axis, which is simply a mass of twisted longitudinal fibres. From this axis pass the numerous fine threads, each with its adhesive disc, which go to form the main external part of the byssus or "beard" of the mussel. Williamson is quite decided that the byssus stem is formed independently of these byssus threads, the latter being attached proximally by a ring round the stem and distally terminating in the small adhesive disc which can be attached so securely to the substratum. The thread itself appears to be made up of concentric rings or layers, each of which is somewhat corrugated. Tullberg found that the outer surface of the thread stained with carmine, and concluded from this that it was composed of a different substance from that which made up the central rings, but Williamson thought that this differential staining was due to the action of sea water, which had changed the character of the outer layer. Tullberg also believed that the stem had a rind, but Williamson disproved this and pointed out that an outer covering, although certainly present, was formed by the base of the enveloping threads and was not a differentiation of the stem proper.

(4) Function of the byssus.

Von Nathusius Konigsborn, whose paper I have not consulted ("Untersuchungen über richt cellulare Organismen, namentlich Crustaceen - Panzer, Mollusken-Schalen und Eihullen," 144 pp., 16 Taf. Berlin, 1877), Richel and others held the view that the byssus was a cuticular secretion of the skin as is the Arthropod shell, and that it was shed periodically in the same way. Tullberg, Jobert and Williamson have, however, disproved this theory and demonstrated that the byssus is a glandular product.

The formation of the stem has been described above. It is a continuous growth, but the rate of growth may depend upon the amount of strain that the byssus has to contend with. If the stem becomes cumbersome under too vigorous stimulation, it is cast off and a new one started.

Williamson described the formation of a byssus thread as follows. The foot is extended with its tip attached to the object to which the mollusc is going to fix itself. The stem passes through the groove, which is thus closed in on every side. The secretion then issues along the groove, which it fills, and surrounds the stem. As soon as a thread is in place the groove opens up and the entering sea water hardens the thread. A cement-like secretion from the purple gland collects on the distal end of the thread, which forms the adhesive disc. The thread is white when it is first deposited, but changes to yellow and then to brown. When the threads are very old they are so dark brown as to appear black.

The new byssus threads are often formed so rapidly that the bases overlap and the stem may be greatly increased in thickness, while in other cases the stem may have grown considerably between the formation of one thread and the next and thus a space arises in its length.

Sometimes the thread may break if the pull is too strong, while at other times the disc may not be holding very firmly. A byssus may therefore have some broken threads without discs and some threads with adhesive discs but not attached to a surface. Mussels are frequently found with the adhesive discs and remains of the byssus from other individuals attached to their shells.

If the discs are very securely attached the mussel can and does draw out the whole byssus from its roots.

If the stem grows very much the byssus may get too long and the animal be too loosely attached, in which case new and shorter threads are formed. Williamson suggests that the growth of the byssus is stimulated by the strain put upon it by the byssal muscles.

Field did some experiments with young mussels about 1 inch long at a temperature of 45° F. He used young specimens as they are more adaptable and become more active much sooner than the old ones. Five minutes after being placed in the experimental jars they began to move. When they reached the side of the jars they climbed up them. At the level of the surface of the water they began to form threads on the glass. The first thread took eight minutes to form, the second three, the third five. After four hours there were eighteen threads. According to Lang, the byssus is used as an organ of locomotion by those species which possess it in that they alternately attach and release the byssus threads. Perpendicular glass surfaces can be climbed in this way and it has also been noted that horizontal progress over mud can be performed in the same manner.

Several authorities have worked on the chemistry of the byssus and I quote Field for a summary of their views. Krukenberg (1886) considered it to be composed of a material allied to conchiolin, Alderhalden (1908) found it to belong to the albuminoid group and Hammarsten (1914) classified it as a skeletin compound in the group of albuminoids.

Atkins described several abnormalities of the foot, the commonest being the presence of a rudimentary accessory foot near to the base of the normal one. The secondary foot is pigmented but is without a ventral groove or anterior sucker. The position of the foot is also subject to variation and has once been found anteriorly placed.

DIGESTIVE SYSTEM.

(Figs. 5, 6, 7, 8, 9, 15, 16, 17, 20, 21, 26, 28, 29.)

A. The Gills.

The gills are described under this section since, although there is some doubt about their respiratory function, there is none about their alimentary. The gills are the means used for the capture of the plankton and the organic debris which form the food. All Lamellibranchs have a pair of ctenidia, or gills, hanging in the mantle cavity between the mantle and the visceral mass. These ctenidia are primitively somewhat posterior in position and extend forwards to a greater or lesser extent in the different species. Each ctenidium consists of a hollow axis extending roughly parallel with the antero-posterior axis of the body. Filaments, which are hollow prolongations of the axis, descend at right angles to it into the pallial cavity, the sum of all the filaments forming the flat surface or lamella of the ctenidium.

Structural differences in the ctenidia are the basis of classification of the five orders of Lamellibranchs. The Protobranchia have a single pair of plume-like ctenidia, each with two rows of filaments. The Filibranchia have two pairs of plate-like gill-lamellæ formed of V-shaped filaments and these filaments are united or joined by means of interlocking cilia—that is, the interfilamentar junctions are ciliary. Bridges between the lamellæ of the same side, the interlamellar junctions, may or may not be present. The Pseudo-Lamellibranchia have gills plaited so as to form vertical folds, the interfilamentar junctions may be ciliary or absent, and interlamellar junctions are developed. The Eulamellibranchs have gill filaments which have both interfilamentar and interlamellar junctions vascular in structure. The Septibranchs have gills which are reduced to a horizontal muscular strip.

The order Filibranchia, to which *Mytilus edulis* belongs, is characterised, firstly, by the nature of the gills, which are formed of parallel reflected filaments—that is, the parallel filaments of each gill are turned up on themselves to form double gill lamellæ so that there are apparently four gills on each side. The lamella of the outer gill is reflected outwards (*i.e.* lateralwards), but the lamella of the inner gill is reflected in the opposite direction (*i.e.* mesialwards). The two contiguous gill faces are therefore the unreflected portions of the two gills. This unreflected portion is termed the descending lamella, and the reflected portion the ascending lamella of the gill. Hence, taking a section across the animal in this region (fig. 16), one would get first the mantle, next the outer or ascending lamella of the outer gill (A.BR.O.), next the inner or descending lamella of the outer gill (D.BR.O.), next the outer or descending lamella of the inner gill (D.BR.I.), then the inner or ascending lamella of the inner gill (A.BR.I.), and finally the visceral mass. On the other side of the visceral mass the same condition is found.

Secondly, the Filibranchia are characterised by the mode of union of the gill filaments. These bear discs at intervals along their length which are covered with cilia (C.J.). The ciliated discs of adjacent filaments are opposed to one another, and in life the cilia interlock with one another. A firm interfilamentar junction is thus formed. About thirty discs occur on the filaments of the ascending lamella and about forty on the descending one. These discs are not on the centre of the long axis of the filament, but are much nearer the adjacent lamellæ of the same side. This structure can be readily made out in a transverse section of the gills (fig. 17). A union between the outer and inner lamellæ of each side is present in some Filibranchia. The existence of these interlamellar junctions (fig. 16) is a feature of the sub-order Mytilacea to which *Mytilus edulis* belongs and distinguishes it from the other sub-orders of the order. In *Mytilus edulis* there are sometimes three but usually four of these interlamellar junctions (fig. 16, I.L.J.) to each filament. They are composed of muscular fibres surrounded by epithelium and contain a canal which is continuous with the branchial vessel or hollow cavity (B.V.) in the gill filament.

The upper edges of the filaments of the outer or ascending lamellæ are hook-shaped and are united with one another by tissue, and through the organic continuity thus formed there travels a blood vessel, the efferent branchial vein (EFF.BR.). This continuity can, however, be broken with a certain amount of ease. The upper edges are quite free otherwise—that is, there is no connection between them and the visceral mass, on the one hand, or the mantle, on the other. Further, interlamellar junctions are not found as high up on the gill as this, so that the upper edges are not united to the descending or inner lamella of the gill.

Each filament consists of a single layer of epithelial cells many of which bear specialised cilia, that is, cilia of given length and capable of lashing in a certain fixed manner so as to cause currents of stable direction.

The epithelium surrounds a central canal, the branchial vessel (B.V.). Kellog reports the presence of gland cells in the latero-frontal region, but Field is doubtful of their presence and the writer has not been able to demonstrate them. The central canal is lined with a tissue which does not show cellular structure under the microscope. Kellog and Peck both consider this to be chitin, but Field believes it to be conchiolin or some related substance. Mitsukuri, working on *Nucula,* found that the substance was insoluble in weak acids and alkalis. He isolated the framework by treating the gills of *Nucula* with weak caustic potash, and stained it with carmine and other colouring matters. At any rate, there is no difficulty in obtaining good sections of the filaments by cutting, with a microtome, material which has been fixed in Bouin's fluid and has not been specially treated for chitin. These authors all report the absence of this disputed material from the canals of the interlamellar junctions.

The arrangement of the cilia on each filament of the outer and inner lamellæ of each gill on the two sides is as follows (fig. 17). The terms "outer" and "inner," as applied to the face of the filament, are used for the faces away from and towards the adjacent lamellæ of the same gill. That is, outer, when referring to the outer or ascending lamella, is the lateral face of the filament towards the mantle, whereas in the inner or descending lamella it is towards the mesial face and therefore facing the descending lamella of the other gill of the same side, the gills being considered as back to back, with the inner faces approximating and the outer faces away from one another.

(*a*) A row of short frontal cilia (F.C.) on the outer side of the filament.

(*b*) A small patch of very long latero-frontal cilia (L.F.C.) on the postero- and antero-lateral corners of the filament.

(*c*) A short row of long lateral cilia (L.C.) on the anterior and posterior faces towards the outer side.

(*d*) A row of small ab-frontal cilia (A.F.C.) on the inner side of each filament.

The nerve supply to the gills and the circulation of the blood through them is dealt with in the sections devoted to the Vascular and Nervous Systems.

Each ctenidium commences at the extreme anterior end of the body between the outer and inner labial palps. It extends backwards, united with the inner side of the mantle, and terminates at the branchial membrane at the posterior end of the body. The filaments are short at the anterior and posterior ends and are much more elongated in the area between a point half-way along the anterior byssus retractor muscle and the anterior side of the posterior adductor muscle. The consequent structure is shaped like a hollow crescent tapering at both ends. On no part of its length is the outer lamella of either gill attached to any part of the body, and hence there is no organic formation of an epibranchial chamber to separate the outgoing current from the entering current in the branchial chamber.

Along the free edge of the gills, where the descending lamella turns upwards to form the ascending one, there occurs a longitudinal hollow termed the food groove (F.G.).

Atkins has shown experimentally that regeneration of the gills occurs, and that the time taken may be less than eight months, but that the regeneration of the whole gill is not invariable, as new growth may be restricted to the formation of a food groove only. Atkins notes that even when size of mussel, method of cutting, position of cut on gill and conditions in mussel's health were the same, at the end of the experiment the degree of regeneration was varied.

B. **The Alimentary Canal.** (Figs. 6, 7, 8, 9, 20, 21.)

[DISSECTION.—*For dissection of the alimentary canal, it will be found easier to use an animal which has been preserved. In the fresh specimen it is rather difficult to separate the intestine from the digestive gland. Remove the animal* *from its shell and pin it in a dish with the dorsal side uppermost. Remove the mantle overlying the heart and also cut away the pericardium. Cut into the ventricle and, carefully stripping it away, follow the rectum to the anus. On top of the posterior adductor muscle there will be found the direct and recurrent intestines, and it will be a fairly simple matter to follow these forwards. To trace the direct intestine under the heart it will be necessary to push the rectum to the left and remove the ventral wall of the pericardium. The intestines will then be seen easily in a specimen which is not filled with genital products. In a mature specimen it will be necessary to brush away the gonads. Anterior to the heart, the stomach and intestines will be found to be embedded in the tissues of the digestive gland and in order to expose them one should gently tease the loose tissues away with forceps, needle and a fine brush. This dissection is made very simple if one first injects colouring matter into the gut through the mouth and the anus, but this should not be necessary in a well-preserved specimen. Figs. 7 and 9 should be studied while the dissection is in progress.*]

THE PALPS.

Labial palps are present in most Lamellibranchs. They are flattened prolongations of the lips and are variously shaped, though usually triangular. There is a pair on each side of the mouth opening.

In *Mytilus edulis* the palps are long and thin (figs. 20 and 21, I.L.P. and O.L.P.). On the mesial face of the outer and the lateral face of the inner—that is, on the opposed faces of the two palps—there runs a longitudinal ridge. The ridge extends from the corner of the mouth along the centre of the palp to its tip. From this ridge there extends a series of fine parallel ridges to the ventral edge of the palp. The palps are covered with a ciliated epithelium. The inner palps are attached to the visceral mass for part of their length, while the corresponding portion of the outer palp adheres to the mantle.

THE LIPS.

The lips border the mouth in practically all Lamellibranchs. The outer palps unite to form the dorsal or anterior lip (D.L.) while the inner form the ventral or posterior lip (V.L.).

THE MOUTH.

The mouth (M.) is wide and much compressed dorsoventrally, so as to make it almost slit-like. Two bands of very long cilia pass from the corners of the mouth obliquely backwards to converge on the œsophagus (fig. 6, C.B.) Salivary glands are not present, and these structures have not been demonstrated in any Lamellibranch.

THE ŒSOPHAGUS.

The œsophagus (ŒS.) passes posteriorly, going somewhat dorsally, as it does so, through the digestive diverticulum. It extends from the mouth to the anterior end of the stomach.

THE STOMACH.

The stomach (STOM.) is an oval structure which frequently has small dorsal, ventral and lateral diverticula. A large ventral diverticulum is often but not invariably present. This, when it is developed, opens from the stomach near the point of entry of the œsophagus, but while the œsophageal communication is median that of the diverticulum is ventral. This diverticulum may extend backwards ventral to the stomach as far as the level of the beginning of the intestine.

The lining of the stomach is thrown into grooves and ridges, and a particularly large groove runs in a zigzag line along the ventral side of the stomach. It is continued into the intestine (fig. 8). Opposite the point of entry of the crystalline style (see below)—that is, opposite the opening of the direct intestine—there is found a thin, transparent structure of the consistency of cartilage. Pelseneer, in Lancaster's Treatise, describes it as the cuticular lining of the stomach. It had not been otherwise named in the English language until Nelson called it the gastric shield. (See below.)

The stomach is entirely embedded in the so-called liver, digestive gland or digestive diverticulum and it is not easily isolated without breaking its walls. Numerous wide ducts put the stomach and the digestive gland in communication with each other. They are present both ventrally and laterally and frequently connect with grooves in the stomach. The number varies between eight and fourteen.

THE DIRECT INTESTINE.

The intestine proper is divided into three parts, of which the first is the so-called direct intestine (figs. 7, 9, D.I.). It passes from the posterior end of the stomach and is embedded in the digestive tissue emerging from it at the level of the heart. It travels backwards ventral to the pericardium and the rectum and is therefore in the middle line. The direct intestine follows a straight course in a postero-dorsal direction. When it reaches the posterior adductor muscle it passes dorsal to it, lying directly upon it. When half-way across the muscle, the direct intestine bends sharply to the right and then again at right angles parallel with the straight intestine. This portion is the recurrent intestine. There is a small blind sac at the bend, the crystalline style cæcum (CÆC.). In this cæcum lies the posterior termination of the crystalline style.

In a well-nourished specimen and one that has not been kept for any length of time under abnormal conditions the crystalline style occupies the whole length of the direct intestine, and lies on the ventral side of it. The style can only be found, as stated, in a very fresh specimen. In an individual which has been kept alive in fresh sea water but deprived of food, the style becomes so much reduced in size that it does not fill that part of the direct intestine which it occupied in the living and feeding animal. Very frequently, after a short time under conditions of deprivation it disappears completely. Bruce suggests that lack of oxygen is contributary to its disappearance.

The direct intestine has its lateral walls projecting inwards as a typhlosole, with a consequent division of its cavity into two regions of unequal size. The larger of these divisions contains the crystalline style. The projections which divide the lumen of the intestine are brought about by an increase of size in the columnar epithelium of the walls. These are of interest when one compares the intestine of *M. edulis* with that of other forms. In the Protobranchs there is no such partial separation of the intestinal cavity into two parts, and the style lies in the cavity of the direct intestine. In many of the more highly evolved Lamellibranchs that part of the intestine containing the style is completely cut off from the rest of the direct intestine and forms a separate blind diverticulum, the crystalline style cæcum. In the Filibranchs there are gradations between these two. Where the infolding of the wall is strongly marked it is correlated with the presence of the small sac at the posterior end of the direct intestine, as in *M. edulis*. In other members of the genus this is much larger. In *M. latus*, Purdie describes a very long diverticulum. It is remarkable that there is a similar series amongst the Gastropods, where the primitive species have no differentiated style sac while the more advanced ones have.

The crystalline style is of a colloidal nature resembling mucin. It contains an enzyme or enzymes with strong powers of digesting starch, and is easily soluble in cold water, less so in salt water, and is coagulated by boiling water, alcohol and other protein precipitants. The KCN test for albumen gives positive results. Mitra calculated the composition as 88 per cent. water, 12 per cent. globulin, 1 per cent. salts. Nelson describes the following as the mode of formation of the crystalline style. Mucus is discharged into the small diverticulum at the apex of the direct intestine and then carried along by cilia towards the stomach. As it goes the secretion is laid on from the cells of the projecting part of the gut. The long cilia of the larger part of the intestine beat on this mass of mucus and style secretion, thus forming the style. As it slowly travels towards the stomach, the style is rotated by these cilia. Normally there is no food in this dorsal part of the direct intestine, but in an animal which has been starved with consequent disappearance of the style and then fed very liberally, food particles are freely incorporated with the mucous core. This indicates that the gut must have been so full that food will have overflowed into that part of the cavity normally occupied by the crystalline style. Several experimenters have shown that food is not necessary for the formation of the crystalline style, and Nelson thinks it probable that it may arise as a response to siphoning regardless of the presence of food in the incoming current. Under suitable conditions it is regenerated in quite a short time. Very little information is available about the development of the style, but it is clearly marked in an oyster 4 mm. in diameter.

The crystalline style has been studied for some time and many theories have been offered as to its probable function. Amongst these it has been interpreted as a vestige of a visceral skeleton, a masticatory structure comparable with the radula of Gastropods, an aid to absorption by pressing the food against the intestine, a prevention of a too rapid flow of bile by blocking up the bile ducts, a reserve of nutriment, a food store for parasites useful to the host or for the development of sex organs and the promotion of breeding, and a means of incrusting foreign particles, thus rendering them harmless. Anton de Heide, discoverer of the style, suggested in 1686 that it secreted a digestive fluid. Coupin in 1900 investigated the nature of the enzymes and found amylolytic ferments, much amylase, and a little sucrase in a mucilaginous matrix.

Nelson ascribes three functions to the crystalline style. First, as it slowly rotates in the stomach it stirs the food about, keeping it in motion and sorting out larger foreign particles which would sink. In this way it acts as a substitute for peristalsis. The second function is that of collecting undigested food and putting it in the core. This could act as a store during periods unfavourable for feeding. The third function is that of supplying a ferment for the digestion of starch. According to Nelson, a copious supply of this would be necessary for an animal with food that contains an abundant supply of this substance. Under this interpretation of the function of the crystalline style, the gastric shield is of use in protecting the lining of the stomach from the rotating head of the style. The style might be distinctly abrasive in this way if it had a covering of foreign matter.

THE RECURRENT INTESTINE.

The recurrent intestine (figs. 7, 9, R.I.), is the part of the intestine which passes forwards from the direct intestine at its junction with the crystalline style cæcum.

The recurrent intestine travels parallel with but to the right of the direct intestine. It lies just ventral to the pericardium on its right-hand side and may or may not be completely covered by it. Just anterior to the pericardium the recurrent intestine passes over to the left, crossing the direct intestine and the rectum dorsally. It becomes enveloped by the digestive tissue and continues forwards ventral and to the left of the stomach, descending as it nears the anterior end of the animal. It crosses over to the right again, passing dorsal to the œsophagus as it does so, and then turns round in a fairly sharp curve and passes under the stomach in a posterior direction. Passing dorsalwards behind the stomach, it travels backwards to merge into the rectum.

THE RECTUM.

The rectum (figs. 7, 9, RECT.) is the posterior part of the alimentary canal and runs in a straight line to the anus. The rectum enters the pericardium and the ventricle of the heart at their anterior ends and somewhat to the left of the middle line. It apparently traverses the whole length of the ventricle and can be seen as a broad tube within it, but morphologically this is not the case, as the heart in its development surrounds the rectum but does not enclose it. The pericardium, ventricle and rectum each have their own individual walls with space between them, but these spaces are so constricted that they appear to be non-existent. Fig. 26 shows a section through the heart and rectum and there is a line drawn round the latter which represents the inner walls of the ventricle and pericardium. The rectum leaves the heart at its posterior end in the middle line, and then passes backwards over the posterior adductor muscle. It lies along the direct and recurrent intestines. It opens to the exterior at the anus, which lies on the ventro-posterior side of the muscle. The anus is somewhat more muscular than is the rest of the rectum, and is coloured by brown pigment. The fæcal matter is expelled as more or less cylindrical pellets which may form ribbons.

C. **Histology of the Alimentary Canal.** (Figs. 26, 28, 29.)

The mouth is lined with a ciliated columnar epithelium, beneath which is a broad basal layer of gland cells. The whole is surrounded by a narrow layer of mixed longitudinal and circular muscle fibres.

The œsophagus is similarly constructed, except that the region of gland cells is larger and there is a basal layer of loosely packed cells between the gland cells and the muscle layer.

The stomach wall consists of an inner columnar epithelium of very tall cells bearing comparatively short cilia. Some mucous glands are present, and the basal layer on which these lie varies in thickness. It is more developed in the floor of the stomach, where the larger folds are present. The muscles surrounding the stomach are composed of mixed fibres, with the longitudinal ones predominating.

Lining the stomach along the dorsal side is the homogenous substance, the gastric shield, beneath which no cilia can be seen.

The direct intestine has its cavity divided into a larger and a smaller portion ; the larger may be dorsal or ventral according to the position where the section was taken, and is lined by a short ciliated columnar epithelium the cilia of which are very long and plentiful. This is bounded by a very thin layer of mixed circular and longitudinal fibres. Goblet-shaped mucous glands are intermingled with the epithelium.

The projection of the lateral walls which partly divides the cavity into the two portions is brought about by the sudden and very great elongation of the columnar epithelium. On the projections the cilia are more scantily developed, but there is a greater development of the mucous and glandular cells. The remainder of the wall of the direct intestine consists of gland cells and a few small ciliated columnar epithelial cells. This is the portion that lines the smaller cavity.

The recurrent intestine has a characteristic structure. It is flattened on one side and semi-circular on the other. The flat side is composed of very tall, ciliated, columnar epithelial cells, but along the middle line of this region there occur a few shorter cells so that a furrow is formed. At each side of the flat part, where it passes into the more circular, the tall cells change rapidly into a region of much shorter cells of the same form. At the middle of the circular area the cells are again elongated, but not to the same extent. Gland cells are present and there is a very narrow band of mixed muscle fibres.

The rectum has the same semi-circular outline as the recurrent intestine and there is a corresponding arrangement of the constituent cells, but the tallest cells do not differ so markedly from the rest. The furrow, on the other hand, is much deeper. Cilia are long but are scantily developed.

D. The Digestive Gland.

The so-called liver, digestive gland or digestive diverticulum (D.G.) is a mass of yellowish or brownish-green tissue which occupies the larger part of the anterior region of the visceral mass. In a mature specimen it closely intermingles at its edges with the gonad.

A transverse section of the tissue shows it to be composed of a series of blind ducts of varying calibre which unite with one another and finally converge on the stomach, into which some of the largest ones open. The walls of the ducts are made up of a somewhat irregular ciliated epithelium. Between the epithelial cells are rounded cells which stain deeply with eosin when young, but as they become older they are more vacuolated. The fresh tissue is very deeply pigmented, and this pigment in *Mytilus edulis*, according to MacMunn, does not occur in the cells as it does in *Ostrea*, but is scattered at random in the connective tissue between the tubes of the gland. He suggested that these pigment granules have been deposited by absorption from the intestine and have not been secreted by the gland. They can also be seen in the lining epithelium of the alimentary canal. The granules are very small and are coloured brown. The brown is due to the presence of a substance that MacMunn calls "entero-chlorophyll," which is nearer in composition to plant chlorophyll than to any other pigment. Entero-chlorophyll is deposited in the gland with other reserve products and fat is instrumental in its deposition.

List made experiments on this gland and found that the granular cells take up food materials, and also experimentally fed particles, such as indian ink. On the cells becoming filled, particles were returned to the stomach and intestine. List found that the colour of the gland is dependent on the nature of the food.

Yonge fed molluscs with a suspension of iron saccharate, and after sectioning found this lying within the vacuoles of the digestive gland cells. He asserts that this so-called liver tissue acts as an organ of absorption and intracellular digestion and that it possesses none of the functions of a liver or pancreas.

Both Daniel and MacMunn failed to find any glycogen in the digestive gland to indicate food storage corresponding to that of the liver. Daniel found the fat content of the gland relatively high and MacMunn asserts that the gland apparently forms fat and certainly stores it ; he also gives it an excretory and a ferment-producing function. He says : " One by one its pretensions to the ' hepatic ' function have been removed, and it finally has emerged from the discussion as simply a pancreas."

Daniel noted that most colour was present in the organ when plankton was at its maximum and algal spores really abundant.

E. The Mechanism of Feeding.

This subject has been studied in recent years in various Lamellibranchs. A successful method of investigation is to cut the posterior adductor muscle and then to separate the two valves. After leaving the animal to recover from the shock, inject carmine particles into the mantle cavity under sea water. The ciliary currents can then be observed.

It has already been stated that the main inhalent currents are brought about by the agency of the lateral cilia which beat across the length of the gill filament. Food particles are collected from this by the frontal cilia on all the lamellæ and conducted towards the food groove at the free edge of the gills. Within the food groove they meet an anteriorly directed current and are carried towards the mouth. The smaller particles are thus carried, all the larger ones having dropped from the gill lamellæ to the mantle surface. These small particles travel forward until they reach the anterior end of the body, where they encounter the smooth side of the palps. They cross these to the dorsal side and then are carried over to the ridged sides of the palps. Selection occurs here and the smallest particles are carried along the ridged surface to the mouth. Only very small particles are thus carried; any that are too large either cross the palp completely to the ventral side and are carried along the ventral edge to the tip of the palp, where they drop off on to the mantle, or else they pass out of the groove between the palps, where they would also drop off. Any food material which has come from the inhalent current and encountered the visceral mass posterior to the foot also falls on to the mantle.

There is a second anteriorly directed current at the angle between the gill axis and the mantle over the external plicate canals. Particles in this are carried very slowly towards the mouth if they are sufficiently small, but there is a ready tendency for them to encounter a ventrally directed stream on the mantle which starts only just below the anteriorly directed current.

The mantle is the organ for the elimination of large particles. It is very sensitive to contact and undergoes considerable contraction if stimulated very lightly. These contractions would readily dislodge and eject particles from the mantle and from the mantle cavity.

The branchial membrane is probably of service, also, in throwing particles downwards from water currents.

During feeding under experimental conditions a great deal of mucus is formed. Graham on *Solen* suggests that this makes the small particles adhesive and forms large particles for rejection, but it also tends to waste those that should be utilised. This, however, will probably only take place to an important extent when a large quantity of mucus is formed, either during experimental conditions or when the water is in an unhealthy condition, and where rejection of *all* food is necessary.

Food particles in the stomach are further graded, the small ones being carried dorsalwards, mixed with style secretion and carried to the digestive gland. Larger particles travel along the groove on the floor of the stomach and along the smaller lumen of the intestine to be discharged finally at the anus.

Dodgson calls the particles which are discharged from the mantle without having entered the alimentary canal *pseudo-fæces*. The pseudo-fæcal ribbon is mixed with mucus and in appearance is very like a fæcal discharge, but when it is continuous it may be as much as several feet long, whereas the fæcal ribbon is always short. More frequently, however, the pseudo-fæces form a flocculent mass of irregular outline.

The fæces themselves pass through the exhalent siphon, whereas the pseudo-fæces are discharged just below the branchial membrane, the presence of which tends to force them downwards. The fæces pass from the exhalent siphon in the form of a ribbon from 0·75 to 1·5 mm. wide, which is marked with a longitudinal ridge. The colour varies with the food from dark brown to slate colour and sometimes white. The fæcal ribbon may be as long as 1·5 to 2 inches and is shot out by the exhalent current some 2–3 inches.

RESPIRATORY SYSTEM.

(Figs. 5, 16, 17, 28, 29.)

Structure and Function.

Respiration in *Mytilus edulis* is brought about by the agency of several organs. (i) Gills. (ii) Membrane at the base of gills. (iii) Surface of body.

(i) GILLS.

For a description of the structure of the gills, see the section on the digestive system. The gills in Lamellibranch molluscs perform a double function, but that of capturing and transporting the minute organisms on which the animal feeds is the primary one. Respiration is secondary only, since there is not a complete branchial circulation (see **Circulation of the Blood**) ; hence the structure of the gills is dealt with elsewhere.

The gills are certainly necessary for the movement of the respiratory current. Water is drawn in through the ventral side of the posterior edge of the mantle cavity. The chief cause of the inhalent current is considered by Orton to be the lateral cilia, and these are aided by the ab-frontal cilia (fig. 17, L.C. and A.F.C.). The movement of these cilia is such as to cause a current across the length of the filaments (that is, parallel with the gill axis). The exhalent current passes along the dorsal side of the lamellæ in the area below the plicate surface of the mantle and between the inner and outer gill lamellæ. Union of the mantle folds posteriorly forms a dorsal exhalent siphon.

There is thus no doubt but that the gills are necessary for respiration, but how far their work is more than mechanical it is difficult to estimate. Knowledge of the nature of the lining of the branchial vessel is necessary before one can evaluate further their work. If this lining (fig. 17) were chitin, the passage of gases would be resisted, but otherwise it is difficult to see how the gills could avoid being respiratory. The sea water is outside with its dissolved oxygen and the blood is within. Until one knows the nature of the separating membrane, one cannot estimate the rate of passage, if any, of the gas.

Sabatier considered the circulation within the gill filaments to be imperfect owing to the small cross-section of the filaments, the pressure of the blood being low, having already traversed the kidney or other capillaries, and the presence of other and larger vessels allowing blood to return to the heart without passing through the gills.

(ii) PLICATE MEMBRANE.

The *Organes godronnés* of Sabatier are thin folds of connective tissue lying in the angle between the mantle and the gills (fig. 26, P.M.) Longitudinally they extend the whole length of the gill axis. They are covered with a fine ciliated epithelium and enclose a blood vessel which connects the mantle veins with the renal and longitudinal veins. These plicate membranes are the principal and most reliable means of respiration.

(iii) SURFACE OF THE BODY.

The mantle, when the reproductive organs are dormant, is an accessory organ of respiration, but when these are functional the consequent loading of the mantle with genital products is a hindrance to free gaseous exchange between the blood and the water in the mantle chamber. During the reproductive period, the respiratory function of the plicate canals is increased. They become enlarged and the flow of blood through them is greater.

BLOOD VASCULAR SYSTEM.

(Figs. 7, 15, 16, 17, 19, 20, 21, 22, 23, 24, 25, 27.)

The vascular system of Lamellibranchs is, like that of the rest of the Mollusca, an open one. Many of the vessels are wide and capable of a great deal of variation in degrees of contraction and dilation. Venous sinuses of considerable dimensions exist, but have connective tissue walls, though they may lack an endothelium. Lacunar tissue is abundant.

There is a dorsally placed heart consisting of three chambers, a median ventricle and paired lateral auricles. The ventricle always has very muscular walls, while the auricles very seldom have more than a slightly developed musculature. This heart generally lies in a pericardium with which it never has any open communication. The pericardium, with the enclosed heart, is situated on the dorsal side of the animal and is penetrated by the rectum. The position of the ventricle in relation to the rectum varies, being either ventral to, dorsal to, or traversed by this part of the alimentary canal, the last condition being the one most usually found. There is generally a connection, the reno-pericardial duct, between the pericardium and the kidney. There may or may not be an open communication between the right and left auricles.

There are generally two aortæ in Lamellibranchs which arise from the ventricle, one the dorsal anterior and the other the posterior ventral, but in a few species the posterior aorta is very much reduced in size, and in others where the siphons are absent or only developed to a slight extent there is but one aorta, the anterior. Where both are developed, the posterior supplies blood to the posterior part of the mantle and the posterior adductor muscle, while the anterior distributes to all the rest of the body.

In species with a well-developed foot and siphons, or with siphons alone, valves are present at the origin of the aortæ and sometimes at the root of the posterior aorta. These prevent blood from being driven in a backward direction towards the heart when the foot or siphon suddenly contracts.

Blood which has been distributed to the organs of the body finally reaches the venous sinuses, of which there are three main ones, the pallial, the pedal and the median ventral sinuses. From these blood is carried to the kidneys, thence to the gills and finally back to the heart by the oblique vein, which opens into the auricles. From the auricles it passes through the auriculo-ventricular communication to the ventricle.

The blood is, with very few exceptions, colourless, and contains nucleated amœboid corpuscles. Some species also have non-amœboid corpuscles containing hæmoglobin, while others have hæmocyanin corpuscles.

[DISSECTION. *It is necessary to inject the blood vessels before their distribution can be followed out. Where the arteries are concerned, it is a comparatively simple matter to insert a fine cannula into the beginning of the anterior aorta or into the ventricle and inject with a steady pulsating movement. It is best to use an animal that has immature gonads and remove one valve of the shell only. This will help to keep the specimen in normal shape until the injection mass has cooled or been precipitated. Inject with the cannula pointing anteriorly. The veins are not easy to inject, and it is important to have a specimen with immature gonads. Various points of attack are required.* (1) *The foot.* (2) *The posterior side of the posterior adductor muscle—inserting the cannula into the muscle between two bundles of fibres.* (3) *The point where the horizontal vein receives the anastomosing vein. Direct the cannula both forwards and backwards.*

The best injection medium was found to be soluble Prussian blue. This is injected into the vessels, and then the specimen is placed in 70 per cent. alcohol to precipitate the blue. A second injection mass used was a solution of Prussian blue in gelatin. The gelatin solidifies on cooling. The objection to the first method is that clogging may take place in the smaller vessels, which then tend to rupture. This was not so serious as the difficulty of getting the gelatin into the vessels before it solidified.]

Mytilus edulis has the usual three-chambered heart lying within the pericardium. It is on the mid-dorsal line just behind the posterior termination of the hinge (fig. 19).

The pericardium (fig. 7, P.C.) is a very thin membrane continuous with the body wall. Laterally it is covered by a part of the mantle which contains none of the ramifications of the gonad. Dorsally it comes to an acute angle, lying between the pallial muscles forming the dorsal approximation of the two halves of the mantle, and ventrally it spreads out somewhat and overlies the direct and recurrent intestines, which can be found just below it. The pericardial cavity is thus roughly triangular in shape. The pericardial cavity opens towards its anterior extremity into wide laterally placed ducts, the reno-pericardial canals (fig. 7, R.P.C.) which communicate with the kidney. The reno-pericardial canal can be seen through the mantle on its external face. It forms with the oblique vein, which lies just behind it, an area in the mantle not usually occupied by gonad, just in front of the place where the retractor pedis muscle passes through the mantle to its point of insertion on the shell. The duct and vein can be seen looped round the muscle, and both pass through the thickness of the mantle before connecting with the visceral mass.

The ventricle (V.) occupies the whole length of the pericardium. It is elongated when contracted, but becomes oval during expansion. That it is capable of further expansion than normally takes place can be seen when it is injected, for it then becomes greatly dilated.

The auricles (fig. 7, AUR.) lie on each side of the ventricle, with which they communicate by a wide aperture (A.V.C.) guarded by a valve which offers no resistance to the passage of blood from auricle to ventricle, but prevents the reverse flow. The auricles are thin-walled elongated sacs with an irregularly lobulated outline. They are covered by the pericardial gland (see EXCRETORY SYSTEM), which gives them a brownish spongy appearance. The auricles do not communicate with one another. Each has a number of small vessels opening into it posteriorly which serve to hold it in position. Laterally they communicate, as seen above, with the ventricle, and anteriorly each is a continuation of the afferent oblique vein of its own side.

As in other Lamellibranchs, the rectum passes through the pericardium. (See DIGESTIVE SYSTEM.) In *Mytilus edulis* it enters antero-dorsally and somewhat to the left side. It then passes into the ventricle and, traversing the whole length of the latter, it leaves both ventricle and pericardium in the middle line posteriorly and dorsally.

Blood Vessels. Arteries.

In *Mytilus edulis* there is a single aorta which arises anteriorly. The ventricle ends blindly posteriorly below the rectum, but anteriorly it gives rise to the single aortic bulb (fig. 19, A.B.). This is a swelling just in front of and below the point where the rectum enters the heart and can be considered as the beginning of the anterior aorta. From it arise two sets of blood vessels, those of the gastro-intestinal region and those which are distributed over the rest of the visceral mass, the foot, gills and mantle. The gastro-intestinal region is supplied by vessels which originate from a short ventral trunk, the cœliac artery (fig. 22, C.A.), which itself arises from the centre of the ventral part of the aortic bulb. All other arteries come off the anterior aorta, which is the direct anterior continuation of the aortic bulb. The anterior aorta (fig. 19, ANT.A.) is the largest artery and may be easily seen, even in a specimen which has not been injected, as a wide vessel in the middle line lying along the anterior dorsal surface beneath the hinge ligament. At a point which varies, but which is frequently just beyond halfway along the straight anterior end of the mussel, it divides at an acute angle into two. The two arteries thus formed are the right and left terminal arteries (R.T.A. and L.T.A.).

Before its division into the two terminal arteries the anterior aorta gives off the following paired arteries (fig. 19).

The posterior pallial artery (P.P.A.) or great pallial artery of Sabatier is a large artery which commences laterally either from the aortic bulb or from the commencement of the aorta. It travels out to the mantle and then descends on its outer face. Very soon after its appearance on the outer surface of the mantle, it divides into a smaller anterior branch and a larger posterior one. The anterior of these branches sends vessels to the liver (these are not shown in fig. 19), and then ramifies in the middle and anterior parts of the mantle, which it supplies with blood. The posterior branch of the posterior pallial artery gives vessels to the liver (not shown either in fig. 19), and then continues posteriorly, giving off vessels to the middle and posterior parts of the mantle. It sends branches to the posterior adductor muscle, and terminates, as do all the other pallial vessels, amongst the pallial muscles at the edge of the mantle.

Hepatic arteries (H.A.). Two or more hepatic arteries originate next from the anterior aorta. These descend through the mantle to the digestive gland, amongst whose diverticula they break up into numerous small vessels.

An intermediate pallial artery (I.P.A.) is given off before the division of the aorta. It sends a branch (H.A.) to the digestive gland and supplies the mantle in the intermediate region.

The anterior ventral artery (A.V.A.) is an unpaired vessel which arises from the aorta just before its division in to the right and left terminal arteries. It is a large vessel which, after its origin from the ventral side of the aorta, runs in the supra-œsophageal cavity beneath the terminal arteries until about halfway between its origin and the anterior adductor muscle. It now turns sharply downwards and crosses the œsophagus either on the right or left side. It continues to travel towards the middle line and passes between the anterior byssus retractor muscles rather anterior to the middle of their length. It is continued posteriorly, lying between the two muscles. It gives two vessels to the liver, a large pedal artery to the foot (PD.A.) and terminates in the byssus and muscles of the byssus and foot.

Shortly after its origin from the aorta, the anterior ventral artery gives off an hepatic artery (H.A.) and at the same time a dorsal tentacular artery (fig. 23, D.T.A.). This runs in the supra-œsophageal cavity for a short distance and divides into a right and a left branch (figs. 20, 23, D.T.A.R. and D.T.A.L.), which pass to the right and left dorsal or outer labial palps. The artery enters the palp on the outer face and travels along the smooth side towards the apex, giving off numerous side branches as it goes.

At the point where the anterior ventral artery passes between the anterior byssus retractor muscles to turn in a posterior direction, it gives two vessels to the digestive gland (fig. 21, H.A.) and a large ventral tentacular artery (V.T.A.). This travels straight forwards until it reaches the level of the middle of the area between the two inner labial palps. Here it divides into right and left branches (fig. 21, V.T.A.R. and V.T.A.L.), which penetrate the palps. These traverse the length of the palp in the same way that the dorsal tentacular arteries do the outer palps.

After the origin of the anterior ventral artery, the aorta divides, but before doing so it may give rise to a second intermediate pallial artery (fig. 19, I.P.A.[2]), the distribution of which is similar to that of the first. Or this artery may arise from the terminal artery after the division of the aorta.

The terminal arteries continue forwards, diverging very slightly from one another. [In fig. 19 they have been separated from one another more abruptly than is usually the case in the specimen. This has been done in order to make the diagram clearer.] During their course the terminal arteries give rise to several vessels. Small vessels pass to the mantle, in addition to the larger intermediate pallial artery, and others to the digestive gland, dorsal and lateral walls of the supra-œsophageal cavity and the anterior byssal retractor and anterior adductor muscles. Each finally terminates in the anterior pallial artery (A.P.A.) which passes anterior to the anterior adductor muscle. The anterior pallial artery, after crossing in front of the muscle, turns backwards and passes beneath it to follow a posterior direction. It sends vessels to the mantle.

THE CŒLIAC TRUNK gives rise to three vessels (fig. 22).

(1) The pericardial artery (PER.A.) is a median unpaired vessel which arises from the cœliac trunk ventrally and passes straight back on the floor of the pericardial cavity, supplying vessels to the pericardium, the direct intestine, the recurrent intestine and the rectum. It finally terminates in small vessels which supply the direct and recurrent intestines where the former passes into the latter.

(2) The gastro-intestinal arteries (fig. 15, G.I.A.) are two wide vessels arising from the cœliac trunk laterally. Shortly after their origin each divides into anterior and posterior branches, the anterior gastro-intestinal artery (A.G.A.) and the posterior gastro-intestinal artery (R.P.G.A. and L.P.G.A.).

The right and left anterior gastro-intestinal arteries are similar in their courses and distribution. They travel on the right and left sides of the stomach respectively, and contribute vessels to it. They also send branches to the digestive gland. In addition, each supplies that part of the intestine with which it is associated—the left one the recurrent intestine and rectum and the right one the recurrent intestine.

Each anterior gastro-intestinal artery, immediately after its origin, gives rise to a large branch which travels posteriorly. This is the right or left recurrent intestinal artery (R.R.A. and L.R.A.). Each runs straight downwards to begin with, mesially to the byssus muscle. Immediately dorsal to the posterior byssus retractor muscle, it divides into several branches, one of which passes forwards to the foot, and others downwards to the mesosoma (fig. 22). The main artery is continued posteriorly, giving branches to the mesosoma as it goes. It reaches the level of the posterior adductor muscle, where it turns forwards again to end in the mesosoma.

The posterior gastro-intestinal arteries differ on the two sides of the body and must be described separately.

The left posterior gastro-intestinal artery (L.P.G.A.) is superficial and passes backwards on the left of the direct intestine, which it supplies with many small blood vessels. It sends a large branch to the mantle (M.G.A.) and it terminates between the direct intestine and the rectum.

The right posterior gastro-intestinal artery (R.P.G.A.) is larger than the left one and much more deeply embedded in the tissues. It passes backwards on the right side of the intestine, between it and the recurrent intestine. It supplies vessels to the right side of the direct intestine and to the rectum. Soon after its origin it gives off a large branch, the intestinal artery (I.A.), which travels posteriorly below and to the right of the recurrent intestine, which it supplies with blood. The right posterior gastro-intestinal artery also gives off some branches from its left side which break up into capillaries on the right of the direct intestine. A branch is sent to the mantle in a manner similar to the one from the left artery (fig. 15, M.G.A.).

Blood-Vessels, Veins.

The venous system of *Mytilus edulis* is complicated in its distribution and not easy to investigate. Careful injection is necessary in order to expose the whole system.

Except for a number of small vessels opening from the mantle through the pericardium and then directly into the auricles posteriorly, all vessels have to return blood to the heart through the paired afferent oblique veins (figs. 7, 27, A.O.V.). The afferent oblique vein comes up from the ventral region of the body. It starts in the longitudinal vein (see below) which traverses the visceral mass at the level of the attachment of the gill axis, and passes upwards and outwards, appearing in the mantle when it has run about half its course. It here lies in the reno-pericardial canal on its posterior side. It opens into the auricle through an aperture which has a valve preventing the backward flow of blood. The afferent oblique vein is frequently covered during the latter part of its course by the pericardial gland.

The following veins form the rest of the venous system:

The marginal sinus (figs. 24, 27, M.S.) is a fairly wide vessel which traverses the whole of the free border of the mantle. It lies in the middle fold of the mantle and receives blood from a series of fine vessels, which collect from the mantle edge only. Behind the posterior adductor muscle, the marginal sinus communicates with both horizontal veins.

The horizontal vein (figs. 24, 27, H.V.) is a paired vessel which lies in the mantle parallel with, but below, the gill axis. It starts anteriorly as a very fine vessel and gets progressively larger as it travels posteriorly to become finally a vessel of considerable size. It has a distinctly sinuous course. The horizontal vein receives the remaining vessels of the mantle, which enter it throughout its course as the ascending pallial veins (A.P.V.). Posteriorly, behind the posterior adductor muscle it communicates with the anastomosing vein (A.V.) and then with the marginal sinus. Along its dorsal side in the anterior and middle regions of the body the horizontal vein connects with the plicate canals through a series of small but very numerous vessels, the plicate canal veins (P.C.V.). Just in front of the posterior adductor muscle, where the plicate canals are no longer developed, there is a communication with the large transverse sinus. Blood returned from the branchial membrane and from spaces between the muscle bundles of the posterior adductor muscle also enters the horizontal vein.

The ascending pallial veins (figs. 24, 25, 27, A.P.V.) are a series of vessels formed from a fine capillary network in the mantle. They open into the horizontal vein throughout its length.

The anastomosing vein (A.V.) is a short paired vessel which runs obliquely across the inner surface of the mantle beneath the posterior adductor muscle. It passes between the transverse sinus, the posterior longitudinal vein and the horizontal vein.

The plicate canal veins (P.C.V.) pass through the plicate canals from the horizontal vein to the longitudinal vein. That is, they start as small vessels from the horizontal vein, pass through the plicate canals and open either into the kidney or into the longitudinal vein.

The longitudinal vein is a large paired vessel which is divisible into two parts by its union with the afferent oblique vein. The anterior longitudinal vein (A.L.V.) is formed at the anterior extremity of the body above the gill axis. It gradually enlarges as it travels backwards and then connects with the afferent oblique vein. The posterior longitudinal vein (P.L.V.) is larger than the anterior. It commences ventral to the posterior adductor muscle and then extends forwards to open into the anterior oblique and the anterior longitudinal veins. These vessels lie dorsal and mesial to the gill and laterally to the cerebro-visceral connective, and are more or less embedded in the tissues of the kidney with which they are in vascular communication. They are the most important sinuses in the body and receive blood from the greater part of the organs. They connect with the kidney, the plicate canals through the plicate canal veins, the anastomosing vein, veins from the mesosoma, visceral veins, intermuscular sinus and branchial veins through the kidney. They collect blood from the mantle through the plicate canal veins and the anastomosing vein, both of which drain the horizontal vein, while the latter drains the marginal sinus.

The visceral veins (V.V.) are very numerous small vessels which carry blood from the visceral mass chiefly to the kidney. The digestive gland is particularly well supplied with these, and an injected specimen will have this organ rendered highly coloured by the presence of the veins both within its substance and on its surface. A considerable number of the external visceral veins from the digestive gland open directly into the afferent branchial vessel.

The inter-muscular sinus (fig. 25, I.M.S.) is superficial. It starts anteriorly on each side between the dorsal and ventral labial palps. It connects on the lateral border of the anterior byssus retractor muscles on each side, with a branch extending between the muscles. It passes over the retractor pedis and the rest of the byssal muscles. Blood vessels from the digestive gland, kidney, foot and mesosoma open into the sinuses.

The mesosomal vein (M.V.) is also paired. It is formed by the union of three main veins from the mesosoma and opens into the transverse sinus.

The transverse sinus (T.S.) lies on the anterior face of the posterior adductor muscle. It is a large vessel which communicates with both the longitudinal vein and the capillaries of the kidneys.

The vessels of the gills consist of a single afferent branchial vessel (AFF.BR.) common to the root of the gill lamellæ on each side, and of efferent branchial veins (EFF.BR.) on the free edge of the gill lamellæ. Thus there is a single afferent branchial vein on each side of the body and paired efferent branchials. Afferent and efferent unite with one another posteriorly, while anteriorly the efferent branchial veins open into the anterior longitudinal vein. Throughout its length, the afferent branchial vessel communicates with small veins from the kidneys.

Circulation of the Blood. (Fig. 27.)

Fig. 27, which is a diagram of the circulation of the blood, is based on a figure by Field which has, however, been much modified.

It will be noted from the above account of the blood vessels in *Mytilus edulis* that there is not a complete branchial circulation. Blood can leave the heart, travel through various organs and then return to the heart without having been near the gills. This is not the usual case in Lamellibranchs, in many of which there is a sinus which transmits the blood to the gills. Sabatier suggested that the condition in *Mytilus edulis* is due to (1) the small size of the branchial vessels, (2) the feeble pressure of the blood, which comes to the gills after having been through a large capillary network, and (3) the presence of a more easy path of return than through the gills. The blood passes very readily through both kidneys and plicate canals. The passage of the blood through the canals is a strong point in favour of the respiratory nature of these structures. Note the presence of large sinuses and an extensive venous system on the superficial parts of body and inner surface of the mantle. This is an aid to gaseous exchange when the mantle cavity is full of sea water. The heart beats in the laboratory at about 30 beats per minute. Auricles contract first, then the ventricle dilates to a slight extent posteriorly, followed by a sharp contraction travelling forwards. The auricle next dilates. A short rest follows and then the process starts again.

THE BLOOD.

The blood of *Mytilus edulis* consists of corpuscles within a colourless plasma. There are three types of leucocytes, all of which, according to Kollmann, are stages in the evolution of one group of cells. When young, these leucocytes contain some granules which take up acid stains readily, and the intermediate stage is clear and absorbs basic dyes. It is while in this stage that division of the leucocytes takes place by mitosis. By the time the leucocytes have reached their maximum size they are completely filled with the granules.

EXCRETORY SYSTEM.

(Figs. 5, 16, 26, 27, 28.)

The Lamellibranch excretory system consists of two separate groups of organs—the kidneys and the pericardial glands. The kidneys are paired elongated sacs with glandular walls which lie ventral to the pericardium, and, except in the Protobranchs, extend as far back as the posterior adductor muscle. Two apertures are always present, one being the orifice putting the kidney in communication with the pericardium—the reno-pericardial aperture. The second is the external opening which leads from the kidney to the exterior, usually through the pallial cavity. A third opening, which is a communication between the right and left kidneys, may or may not be present. In primitive forms, where there is no genital duct, there is a fourth opening by which the gonads communicate with the kidney. In this case the external opening is common to both reproductive and excretory systems.

The pericardial glands, or Keber's organs are developed from the epithelium of the pericardium, and may be on or near the auricles or line the wall of the pericardium.

Mytilus edulis has paired kidneys and paired pericardial glands.

The kidneys (fig. 5, REN.) are dark brown structures extending the whole length of the body from the labial palps to the posterior adductor muscle. They lie dorsal to the gill axis and extend both mesially and laterally to the base of the gills. They appear as a dark brownish-red tissue dorsal to the plicate canals, through which they show. They are most marked mesially to the gills. The kidneys are easily seen in a fresh specimen, but the colour soon fades, and in a specimen which has been preserved even for only a few hours they will be difficult to see, as the colour will have completely vanished. Without the colour, the kidney is not clearly marked off from the plicate canals and from the rest of the visceral mass.

The kidney tissue encloses a central canal which is the collecting canal of the kidney. In the anterior part of the body the kidney tissue is comparatively easily separated from the rest of the body wall, but as it extends posteriorly it becomes more and more intimately connected with the longitudinal vein.

The reno-pericardial canal or sinus (figs. 7, 27, R.P.C.) is situated just anterior to the afferent oblique vein, both being visible through the mantle in front of the pedal retractor muscle. They are most marked in a specimen in which the mantle is filled with ramifications of the gonad, as, being never themselves so filled, they stand out as clear spaces in the surrounding opaque mantle. The kidney is the *appareil urinaire de Bojanus* of Sabatier, while the plicate membranes are the *Organes godronnés* of the same author.

The pericardial glands (fig. 26, P.G.) invest the auricles in *Mytilus edulis* and are of the same colour and appearance as the kidney proper. They are united posteriorly with the wall of the pericardium, and anteriorly they extend down and surround the afferent oblique vein. The glands are shown in figs. 7 and 19, but not named. Cuénot points out that they are true glandular cells in that they are not bathed in blood, but are in contact with it through their fixed bases. Their secretion enters the pericardium itself. Cuénot investigated the function of the excretory organs by injection. He found that the kidneys or nephridia eliminated indigo and that the cells themselves gave an acid reaction. The pericardial glands also gave an acid reaction. Latellier showed that the pericardial glands secrete hippuric acid, which he considered they extracted from the blood. He also pointed out that the kidney extracts water, urea, various nitrogenous bodies, phosphates and possibly uric acid.

MUSCULAR SYSTEM.

(Figs. 1, 4, 9, 18, 26, 28, 29.)

The musculature of the Lamellibranchiata is subject to considerable variation, owing to differing modes of life and the plastic nature of the whole muscular system. Essentially there are three types of muscles. (1) The pallial muscles which comprise the muscles of the mantle and the muscles of the shell. They undergo changes in relation to the presence or absence of siphons, and according to the shape of the shell. (2) The pedal muscles, which are modified in forms where there is a byssus. (3) The intrinsic muscles of the viscera.

The muscles are always unstriped.

The muscles in *Mytilus edulis* can be arranged in six groups without departing from this basic plan:

(1) The adductor muscles of the shell.
(2) The pallial muscles.
(3) The muscles of the foot, extrinsic and intrinsic.
(4) The byssal muscles.
(5) The muscles of the gut.
(6) The muscles of the kidney, ctenidium, etc.

(I) THE ADDUCTOR MUSCLES

The adductor muscles unite the two valves of the shell. There are never more than two of these in any Lamellibranch, and both are present in *Mytilus edulis*. There is, however, a great deal of difference in size between them, the posterior one being very much larger than the anterior. This condition is known as the Anisomyarian, and it is intermediate between the Isomyarian, where the two muscles are equal in size, and the Monomyarian, where there is only one adductor muscle—the posterior. In the Monomyarians the anterior adductor muscle has completely disappeared. All these three conditions are present in the family Mytilidæ. In *Musculus marmoratus* the two adductors are of approximately equal area, though they differ markedly in shape; in *Mytilus galloprovincialis* and *Mytilus minimus* there is a dissimilarity in size, but it is not so marked as in *Mytilus edulis*; in *Mytilus latus* there is no anterior adductor in the adult.

The posterior adductor muscle (fig. 4, P.A.M.) in *Mytilus edulis* is roundish oval or oval in shape. It passes transversely across the animal and is inserted into the right and left halves of the shell. Owing to the way in which the shell tapers postero-dorsally towards its margin, the insertion of the muscle is somewhat oblique. This results in a certain amount of obliquity of the bundles of fibres themselves, and in a more marked variation in their length. The dorsal fibres are obviously the shortest. The posterior adductor muscle is the largest in the body.

The anterior adductor muscle (A.A.M.) is a small flat band of muscle, the greater part of which is embedded in the thickness of the two halves of the mantle. The muscle is inserted into the shell valves at the anterior lower corner.

The adductor muscles draw the two valves of the shell together and hold them so. They therefore act in opposition to the ligament (see **The Shell**). It is obvious that, when one compares the size and position of the two adductor muscles, the posterior one is of far greater importance, and is capable of more work than is the anterior one. In killing a mussel, if one cuts through the posterior adductor muscle, it is a simple matter to separate the two halves, as the anterior adductor offers a feeble resistance. There is no morphological difference to correspond with the physiological separation of the fast and slow fibres which are characteristic of adductor muscles.

Marceau performed an investigation to see if there is any rhythm in the duration of the periods of opening and shutting of the valves, and if the adductor muscles are completely at rest during the opening period. He found that a regular rhythmic series of movements does take place, and that when the shell is opening or shutting a series of graduated opening and shutting movements is going on while the shell gradually becomes more and more open or shut as the case may be. This points to the fact that the muscles are never at rest. Marceau suggests that if they were they would atrophy or tend to do so.

Dr. Paulus Schemenz, in a paper on the means by which starfish open oysters, calculated that a starfish could exert a force of 1,350 grms., which would be quite sufficient to open a Venus shell. This gives some idea of the power with which a bivalve mollusc holds its shell together.

(2) THE PALLIAL MUSCLES. (Fig. 4.)

There is a row of muscle strands along the ventral border of the mantle from the anterior extremity, round the posterior margin, and along the dorsal surface as far forwards as the posterior extremity of the ligament. This, in a specimen 3 inches long, is approximately ¼ inch wide at the point of greatest width, the posterior, becoming narrower as the anterior end is approached. At the level of the anterior adductor they are $\frac{3}{16}$ inch long, and at the ligament they disappear altogether. These muscles are the pallial muscles (PL.M.). They originate in the margin of the middle and inner mantle edges, and are inserted into the shell along a line varying from $\frac{1}{8}$ to $\frac{1}{4}$ inch from the border of the shell. This line of insertion is the pallial line. The pallial muscles are quite simple in *Mytilus edulis*, as there are no siphons.

Other muscles associated with the mantle are as follows: arising from the inner mantle edge in the middle line posteriorly is a band of connective tissue and muscle strands. This is the branchial membrane (figs. 5, 14, BR.M.). It is roughly V-shaped when relaxed and is about $\frac{3}{4}$ inch long. The termination of the membrane is level with the ventral edge of the posterior adductor muscle. The membrane unites the two halves of the mantle together, and continuous with it is the thick circular muscle ring which surrounds the exhalent aperture. This is a simple muscular structure which is flush with the edges of the mantle and not extended into a siphon. Above the branchial membrane are two more folds of muscular tissue which have been named the dorsal and ventral vela (fig. 14, D.F. and V.F.).

A row of intrinsic muscle fibres lies within the mantle on the dorsal side, with its insertion along the line of the gill axis. This row extends from the posterior adductor muscle to the anterior end of the animal, but is more clearly marked at the posterior end. The length of the fibres is at right angles to the gill axis and the longest fibres are about $\frac{3}{8}$ inch. These muscles are of service in twitching the mantle during feeding (see **Feeding Mechanisms**).

(3) THE MUSCLES OF THE FOOT.

For a discussion of the foot muscles in the Lamellibranchs, see the section, EXTERNAL CHARACTERS, **Foot.**

In *Mytilus edulis* the extrinsic muscles of the foot consist of the paired retractor muscle alone (fig. 4, R.P.). The retractor pedis is situated anterior to the byssal muscles. The muscle impression on the shell (fig. 1, R.P.S.) is thus the most anterior of the series of scars between the posterior termination of the ligament and the impression of the posterior adductor muscle. The retractor pedis runs from its insertion in the shell in an antero-ventral direction on each side of the visceral mass. It traverses the anterior byssal retractor muscle externally, and ventral to this muscle it meets its fellow in the middle line to form the extrinsic musculature of the foot. The pedal muscles are round in cross-section, and their insertion into the shell is oblique in that an angle of about 50 degrees is formed with the shell. At its point of insertion, the pedal muscle frequently adheres closely to the most anterior of the posterior byssal muscles, and hence the scar on the shell is oval anteriorly and united with that of the byssal muscles posteriorly. Except for this point of union, the pedal and byssal muscles are completely separate from each other, and after removal of the connective tissue it is possible to remove the foot entire without disturbing the byssus.

On the posterior side of the foot lies part of the byssal gland (see EXTERNAL CHARACTERS, **The Byssus**). It is found between the pedal retractors.

The intrinsic muscles of the foot form a comparatively small portion of the musculature of the foot or of its bulk. There is a thin but compact band of circular fibres which lies immediately under the epidermis, and between the pedal retractors, and surrounding the extension of the byssal gland, is a mass of somewhat irregularly crossing fibres.

The aperture of the byssus apparatus is surrounded by fibres which are continued on to the foot.

(4) THE BYSSAL MUSCLES. (Fig. 4.)

The byssal muscles consist of the paired anterior byssal retractor (A.B.R.) and the double series of posterior byssal retractors (P.B.R.).

The two anterior byssal retractor muscles travel side by side from their place of origin at the byssus along the mid-ventral line towards the anterior end of the body, gradually separating from one another as they pass forwards. At the level of the mouth and just in front of the cerebral ganglia, which lie ventrally to them, they pass through the mantle to be inserted in the right and left halves of the shell respectively. The scar left is either bilobed or elliptical in shape. These muscles are well developed and more or less rounded in cross-section.

The posterior byssal retractor muscles are partially flattened muscular bands which originate with the anterior byssal retractor in the mid-ventral line. The muscles of each side travel in a postero-dorsal direction with varying degrees of obliquity, and, passing through the mantle, are inserted into the shell near to its postero-dorsal margin between the posterior adductor and the pedal retractor muscles. Although constant in position, the grouping of the muscle bundles themselves varies in individuals, on each side of a single specimen, with consequent irregularities in the form of the scar on the shell.

All these muscles are connected with the byssus organ and have no concern with the movements of the foot.

(5) THE MUSCLES OF THE GUT.

The visceral muscles are described in the section on the DIGESTIVE SYSTEM. Both circular and longitudinal fibres are present.

(6) MUSCLES OF THE KIDNEY, CTENIDIUM, ETC.

These organs have scattered muscle fibres.

NERVOUS SYSTEM.

(Figs. 5, 9, 10, 18, 30.)

In the Protobranchia there are four pairs of ganglia, the cerebral, pleural, pedal and visceral, but in all other adult Lamellibranchs there are only three pairs, the pleural having merged completely with the cerebral ganglia. In the development of a good many, however, the four separate pairs of ganglia have been demonstrated.

In Lamellibranchs the cerebral ganglia usually lie dorsal to the œsophagus and their commissure, which is supra-œsophageal, is typically elongated. These ganglia innervate the anterior regions of the body, the labial palps, the anterior adductor muscle, the anterior part of the mantle and the sense organs. The osphradia frequently lie close to the visceral ganglia. They are, however, not innervated by these ganglia, but receive fibres from the cerebral ganglia. The fibres have travelled in the cerebro-visceral connective and split off before it enters a visceral ganglion. The paired cerebro-visceral connectives are always very long and generally superficial, and pass mesially to the renal aperture.

The visceral ganglia, except in Protobranchia, lie on the ventral side of the posterior adductor muscle and are to be found just beneath the outer epithelium. They are primitively connected by a comparatively long commissure. This primitive condition is retained in some families (Anomiidæ and Mytilidæ), but has been lost in many. The visceral ganglia innervate the gills, heart, posterior part of the mantle, and the siphons when present.

The pedal ganglia are connected with the cerebral ganglia by paired cerebro-pedal connectives, but, except in the Protobranchia, there is no pleuro-pedal connective, as the pleural ganglion has disappeared. The pedal commissure is always very short, and in some forms, where the foot is reduced, the ganglia are so closely opposed that the commissure has been eliminated entirely.

Mytilus edulis differs from the typical scheme cited above in several ways. The cerebral ganglia lie beside the œsophagus, although the commissure follows the typical arrangement in being supra-œsophageal. The cerebro-pedal and cerebro-visceral connectives issue from each cerebral ganglion as one large nerve and remain fused in this manner for about half the length of the cerebro-pedal connective.

[DISSECTION.—*The best way of displaying the ganglia and the majority of the nerves is to dissect from the ventral side. After removing the animal from its shell, cut across the mantle on one side only, at about* ⅜ *inch behind the anterior angle, and carry the cut inwards as far as the visceral mass. This enables the anterior region with the anterior adductor muscle to be turned over to one side without damaging the nerves. Pin the animal down in the dish with one pin in the posterior adductor muscle and others in the mantle within the margin of the pallial muscles. Then carefully strip away the connective tissue overlying the anterior retractor muscles. Pick up the fused cerebro-visceral and cerebro-pedal connectives and follow forwards to the cerebral ganglion. To expose the cerebral commissure, it will be necessary to cut through the œsophagus just behind its origin from the mouth* (*fig.* 30).]

The CEREBRAL GANGLIA (C.G.) are triangular structures frequently coloured in the living animal with a bright orange-red pigment. They are the smallest of the ganglia in *Mytilus edulis.* The two ganglia lie up to ½ inch apart, but are connected by a stout supra-œsophageal cerebral commissure (C.COMM.). Each cerebral ganglion gives rise to two large nerves and two small ones, the distribution of which is the same on the two sides of the body.

(I) A large anterior pallial nerve (A.P.N.) which arises from the anterior angle of the ganglion. It runs forwards dorsal to the labial palps and, passing dorsal to the anterior adductor muscle, giving fine fibres to it as it goes, travels towards the mantle margin. It runs backwards in the inner fold of the mantle edge, and gives off a series of fine nerves to innervate this organ. Its largest branch is detached soon after its origin just before the anterior adductor muscle is reached. This, the anterior adductor nerve (A.A.N.) passes on to the ventral side of the muscle, innervating it as it goes. Small branches from the nerve pass backwards to rejoin the anterior pallial nerve.

(2) A fine nerve, the optic nerve (OP.N.), leaves the cerebral ganglion lateral to the anterior pallial nerve and passes through the tissues of the base of the inner labial palp to the eye at the base of the first of the inner gill filaments.

(3) A fine nerve, the buccal nerve (BU.N.) passes from the anterior end of the cerebral ganglion. It distributes to the labial palps fibres which run on the smooth side of the palp, and from which transverse fibres pass across the palp to its ridged side.

(4) The cerebro-pedal connective (C.P. CONN.) and the cerebro-visceral connective (C.V.CONN.) arise as a large common trunk from the posterior apex of the cerebral ganglion. The nerve passes obliquely backwards, traversing the anterior byssus retractor muscle. When it reaches the lateral margin of the muscle it separates into the two connectives. This connection is similar to that seen in Gastropods.

[DISSECTION.—*Cut through the anterior byssus retractor muscle at the point where the two connectives separate. Then cut through the pedal retractor muscle and the pedal ganglia will be exposed.*]

The PEDAL GANGLIA (PD.G.) lie on the dorsal side of the anterior byssal retractor muscle at the point where the pedal retractor muscle crosses it. The ganglia are rounded and coloured in the same way as the cerebral ganglia. The pair lie very close together and the commissure is not seen. Hence at first sight they appear as one, but the line of demarcation can be made out. Each ganglion gives off three nerves to the foot and byssal muscles, the distribution of which is the same for both sides.

(1) The pedal nerve (PD.N.) originates from the ventral side of the ganglion. It passes over the anterior retractor muscle and travels down the foot, which it innervates.

(2) The ventral retractor byssus nerve (V.R.B.N.) arises from the posterior side of the ganglion and travels to the byssus organ and the byssal muscles.

(3) The dorsal retractor byssus nerve (D.R.B.N.) arises from the posterior side of the ganglion and supplies the upper side of the byssal muscles.

The cerebro-pedal connective enters the ganglion anteriorly. Just after its separation from the cerebro-visceral connective it gives off a small nerve to the otocyst, the otocyst nerve (OT.N.).

[DISSECTION.—*Pick up the cerebro-visceral connective where it separates from the cerebro-pedal and follow it backwards to the visceral ganglion.*]

The cerebro-visceral connective is a large nerve. It remains within the connective tissue overlying the visceral mass until the level of the pedal retractor and byssal retractor muscles is reached. It passes ventral to these muscles and then becomes entirely superficial. It is not necessary to remove the epithelium in order to see the nerve. Several fine branches are given off from the connective which pass to the visceral mass, whence they innervate the intestine, digestive diverticulum, kidney and genital organs.

The VISCERAL GANGLIA (V.G.) are triangular and flattened and are coloured in the same way as are the other ganglia. They are the largest of the three pairs and are more separated from each other. The commissure (V.COMM.) connecting the ganglia is stout. From its centre is given off ventrally a nerve, the posterior pedal nerve (P.PD.N.), which runs on the ventral side of the body to the foot. It is a very small nerve and difficult to see.

The cerebral connective enters the ganglia anteriorly, and there are several large nerves which issue from each ganglion. The distribution of the nerves arising from the visceral ganglia is not always the same on the two sides.

The largest nerve is the posterior pallial nerve (fig. 5, P.P.N.). This arises in the postero-lateral angle of the ganglion. It runs obliquely across the ventral side of the posterior adductor muscle, dorsal to the gill axis. At the postero-lateral edge of the muscle it divides into three branches.

(i) The posterior ventral pallial nerve (P.V.P.N.) runs posteriorly through the mantle until it reaches the inner fold of the mantle margin, which it penetrates. It then turns anteriorly and joins the anterior pallial nerve to form the pallial nerve (P.N.). The pallial nerve formed by the fusion of the anterior pallial and posterior ventral pallial nerves is a large nerve which runs the whole length of the free part of the mantle on the ventral side. It is somewhat buried in the inner fold of the mantle, but gives off numerous branches along its whole course which can easily be seen through the outer epithelium of the mantle in those specimens where the mantle is not filled with genital products. The nerve itself can best be found by dissecting on the inner side of the mantle.

(ii) The posterior dorsal pallial nerve (P.D.P.N.) travels dorsally and anteriorly. It unites dorsally with the dorsal pallial nerve. (See below.)

(iii) The siphonal nerve (S.N.) passes straight backwards in the inner mantle folds, where they are fused posteriorly to form the exhalent aperture. It gives off branches to the mantle in this region and finally terminates in the posterior ventral pallial nerve. One of the branches of the siphonal nerve passes into the posterior dorsal pallial nerve.

(2) The dorsal pallial nerve (D.P.N.) is a small nerve which arises from the anterior mesial corner of the ganglion. It travels dorsally along the antero-dorsal surface of the posterior adductor muscle. Towards the edge of the mantle on the dorsal side it divides into an anterior and a posterior branch. The anterior branch sends small branches to the mantle, and in some specimens gives off a branch across the mid-dorsal line to meet its fellow of the opposite side. The posterior branch merges into the posterior dorsal pallial nerve, from which branches are dispatched to the mantle and neighbouring viscera, including the heart and the pericardium.

(3) The posterior renal nerve (P.R.N.) is a fine nerve which runs backwards parallel with, but dorsal to, the cerebral connective for a short distance. It then turns laterally at right angles and runs obliquely dorsalwards in the renal organ.

(4) The branchial nerve (B.N.) is a stout nerve which leaves the ganglion laterally and runs across to the gill axis. It then travels posteriorly in the axis as far as the gill extremity.

(5) The posterior adductor nerve (P.A.N.) is a small nerve given off from the ganglion laterally. It supplies the muscle with numerous fine nerves. Galeazzi found unipolar and bipolar nerve cells associated with the nerve endings on this muscle. A very fine network of fibres is formed which thus results in a very efficient nerve supply in the muscle. Galeazzi considered that this formed an automatic nerve centre which was responsible for the powerful behaviour of the muscle.

Richards (1929) calculated the rate of conduction of stimuli through the pedal nerve of *Mytilus edulis* and, as the result of twelve determinations, using eight animals, he arrived at the figure 92·9 cm. per second at 24° C. with a ± error of 3·3. If a stimulus passed through a nerve ganglion, the average time for nine determinations with seven animals was 0·0087 seconds for 3 mm., showing the rate of conduction to be 2·7 times slower than through a nerve trunk.

SENSE ORGANS.

(Fig. 5.)

The sense organs of *Mytilus edulis* are of six different kinds.

The **Eyes** are persistent larval eyes. They are paired structures and were found by Wilson, in the larval stage when four gill filaments are present, at the base of the first mesial gill filament on its lateral side. They remain unchanged in the adult and are hence very small. The eye is an epithelial invagination containing a lens, and is a true cephalic eye. There are no pallial eyes in *Mytilus*.

The **Osphradia** are a pair of dark brown pigmented patches of tissue situated laterally and ventrally to the visceral ganglia, and mesial to the gill axis in that region.

The **Abdominal Sense Organs** are similar in appearance and lie lateral to the gill axis in the same region.

Both of these sense organs are visible only in a fresh specimen. The osphradia and the abdominal sense organs are the water-testing organs. The former are of general occurrence in the Lamellibranchiata and it will probably be found that this applies to the latter also, though they have not yet been so fully investigated. The structure of these organs cannot be made out without the use of the microscope, and sections should be cut through the ventral part of the posterior adductor muscle close to the visceral ganglia. Both sets of organs consist of a row of cells which are larger than those of the surrounding epithelium, resting upon a basement membrane which contains nerve fibres, and in the case of the osphradia, nerve cells as well. The cells of the osphradia are ciliated, but cilia have not been seen on the abdominal sense organ.

The **Otocysts** are paired structures which lie on the outer epithelium of the ventral side in the angle between the cerebro-visceral and cerebro-pedal connectives after their separation. If an immature specimen or one which has discharged its genital products is narcotised, and the epithelium is then stripped off, it is possible to make a wet mount of the otocyst. The otocyst consists of a round sac, containing granules, continuous with a canal to the otocyst pit at the external opening. The sac is connected with terminations of the otocyst nerve.

Two kinds of **Sensory Cells** occur. In the outer epithelium of the body and the inner border of the mantle are cells sensitive to contact.

The cells containing brown pigment, which are on the ventral border of the mantle, are sensitive to stimulation by light.

REPRODUCTIVE SYSTEM.

(Figs. 5, 7, 10, 11, 12, 13, 16, 26, 28, 29.)

In the majority of Lamellibranchs the sexes are separate, although even in Lamellibranchs that have separate sexes there are isolated cases of various types of hermaphroditism. Only a very few species show any external differences between the two sexes other than that of colour of the genital organs. That is, sexual dimorphism is very rare.

Fertilisation, with the exception of *Ostrea edulis*, where it occurs in the oviduct, is usually considered to take place completely external to the female parent in the surrounding sea water, or else in the pallial cavity of the female.

The system consists of paired superficial gonads which occupy a large part of the visceral mass. They are as a rule posterior to, and surround laterally, the digestive tissue, and as a rule are paler in colour than this tissue. They consist of highly branched tubules whose ramifications extend into the foot and occupy spaces between the bundles of the muscle fibres.

Accessory glands are not known and there is no copulatory organ.

Mytilus edulis has the two sexes separate and the only external difference between a male and a female lies in the colour of the reproductive structures of a mature specimen, those of a male being yellow or cream and those of a female apricot or red. There is also a slight variation in the texture of the ripe mantle.

The reproductive system consists of the usual branched tubes extending through the visceral mass, but the greater part of the organ is in the mantle lobes, which in a mature specimen are almost filled with genital tissue, through which ramify on the outer face the pallial arteries and branches, and on the inner face the ascending veins of the mantle and their factors. A marked difference occurs in the mantle before and after spawning.

In the Mytilidæ the foot is, except for the byssus gland, entirely muscular, and the fibres of the muscles are very close together. As the pedal muscles are the only ones present and the gonad does not penetrate into the foot, there is little need or opportunity for the development of connective tissue through which the ducts of the genital organ could ramify. The byssal muscles occupy a good deal of the visceral mass. Moreover, their position would probably prevent much of the expansion of the gonad which would occur as the genital products reach maturity. With these facts is probably correlated the abnormal presence of the genital canals within the mantle. The Mytilidæ and Anomiidæ are the only families where this extension of the gonad into the mantle occurs. But in *Mytilus edulis* the gonad also fills the mesosoma, spreads over the outer surface of the liver and is particularly thick in the tissues below the pericardium. In a mature specimen the dorso-lateral walls of the pericardium, the foot and muscles, the gills and the thickened edges of the mantle are the only parts not occupied or covered by the ramifications of the genital organ.

The whole gonad consists of paired gonoducts (fig. 10, GON.D.), main genital canals (G.C.), of which there are about five on each side of the body, and very numerous minor canals which terminate in a fine network of small outgrowths, the follicles. Each follicle is lined with germinal epithelium, from which the ova and spermatozoa develop. The rounded male follicles are about the same size and regularly arranged. The female follicles show a considerable variation in size. The largest ones are bigger than the follicles of the male, while the smallest ones are no more than the tapering ends of the minor genital canals.

The minor genital canals are lined on one side by germinal epithelium and on the other by columnar ciliated epithelium (figs. 11 and 12). These canals gradually converge on to the major genital canals, which themselves unite at a point below the expansion of the pericardium in which the auricle lies to form the genital duct. Of the major canals there is one large one from the anterior region of the mantle and liver (fig. 10, G.C.^{1}), one from the middle region of the mantle (G.C.^{2}), one from the posterior region of the mantle (G.C.^{3}), one lying on the floor of the pericardium (G.C.^{4}) leading from the dorsal region of the body and the posterior part of the visceral mass, and one from the mesosoma.

The genital duct passes through the mantle and then, turning posteriorly, runs along the ventral side of the body mesial to and parallel with the axis of its inner gill. It opens to the exterior at the apex of a prominent papilla which lies across the ventral side of one of the posterior byssus retractor muscles, usually the second from the posterior end, but owing to the slight degree of variation occurring in these muscles it is not possible to make a definite ruling on this point. The papilla is common to the renal organ, whose aperture lies on the posterior side enclosed in the angle between the mantle and the genital papilla. The aperture of the genital duct is filled usually with a plug of orange-coloured mucus.

Spawning takes place in the spring, with a second and possibly more important occurrence later in the summer. (See LIFE HISTORY.) Considerable local differences in spawning times takes place.

LIFE HISTORY AND DEVELOPMENT.

Mytilus edulis is unisexual and the production of germ cells by both sexes is enormous. Separation of the sexes can be made out during the breeding season by the colour of the mantle, that of the male being cream-coloured while the female one is darker, sometimes being orange-red. The female mantle is also less granular in appearance. There is a slight preponderance of males over females which is probably in the ratio of about six to five.

At Woods Hole Biological Station spawning individuals have been taken from June to September. At Plymouth spawning has occurred in January, February and March, while specimens from outside sea water examined in May and in August had apparently finished spawning. Stohler quotes Dr. Herbert Sommer (MS.) that *M. edulis* and *M. californianus* (a common American species) also spawn in the winter months. Scott reports that mussels from the Lancashire coast kept in the Piel Laboratory discharged eggs in May, spermatozoa were not seen until June 13th, and spawning lasted until the middle of July, eggs being usually discharged during the night. Although the eggs were always fertilised, no further discharge of spermatozoa was noted. Even eggs which were isolated immediately after they were shed from the parent were found to develop into normal larvæ. Johnstone says that maximum spawning is in July, while there was a secondary spawning earlier in the year, but the number of larvæ produced from this early spawning were very much less than that resulting from the later one. Johnstone also pointed out that there is a good deal of individual variation, and isolated cases occur where spawning is very much earlier or later than the maximum. Lebour found spawning to take place in June, July and August.

Daniel divides the reproductive cycle into three phases. From spawning to early summer there is a short period of rest when the mantle cells form an open network. Reformation of the genital epithelium then follows in the early autumn, with the development of ova and sperms. This is increased to an active formation which ends at the spawning time in the following spring.

Although there is thus a considerable amount of variation in the spawning time of *Mytilus edulis*, there is no doubt that the animal can spawn at one year old.

The ova average 0·07 mm. in diameter and from this Field has calculated that a mussel liberates during a single act of spawning from 5 to 12 million eggs. By comparing the volume of the mantle and mesosoma before and after spawning, he has arrived at the conclusion that a mussel 3½ inches long can produce 25 million eggs. The ovarian eggs are irregular in outline owing to overcrowding of their numbers. The eggs have a large nucleus with a well-defined nucleolus, and an external membrane is present.

The spermatozoa are pin-shaped bodies with an oval head and a long tail. The head terminates in a small conical projection. A male mussel can discharge sufficient spermatozoa to turn the water milky in a trough 10 feet long, 1½ feet wide, and 3 inches deep.

The eggs are discharged in short rods which are pink in colour. These rods fall to the bottom and there break up into the constituent eggs. Sperms are usually discharged at the same time and fertilisation, according to most authorities, takes place in the water. Scott, however, believes that fertilization occurs in the branchial cavity of the female. (See above.)

Field and Wilson have made extensive studies of the development of *Mytilus edulis* and most of the following is based on their results.

The nucleus of the ripe egg, just after reaching the sea water, forms the first polar body, and unless the egg is fertilised within three or four hours development does not extend beyond this point.

The first polar body appears in water at 68° F. within twenty minutes of mixing the eggs and sperms. Only one sperm enters a normal freshly laid egg, and immediately fertilisation has occurred the egg becomes round. This rounding of the egg from the previous irregular shape is a fairly safe assurance that it is fertilised.

The second polar body appears ten minutes after the first, and from now the egg becomes pear-shaped, with the polar bodies at the broad end. Furrows next appear, separating the animals pole into two masses and the nutritive pole into one. The latter enlarges, and one of the animal pole masses fuses with it to form the large cell or macromere. The remaining small mass is then cut off as the first animal cell or micromere. Twenty minutes after the fusion of the male and female pronuclei the micromere has divided once and a third micromere has been formed by division from the macromere. Division from this point is now rapid, the micromeres dividing into two and the macromere giving rise to micromeres. By the time the blastosphere stage is approached the micromeres are enveloping the macromere.

After about another half hour the blastosphere is formed with the macromere almost covered with the micromeres. There is a small segmentation cavity present. When completely enclosed, the macromere itself divides into two large cells which are apparently the beginning of the mesoderm. These two latter divide into more or less equal cells which fill the segmentation cavity. The embryo now becomes ciliated.

Field says that the free-swimming ciliated embryo results normally four and a half to five hours after fertilisation. From this point until twenty-four hours the external changes show rapid multiplication of cells, great development of cilia over the surface and the formation of the long, flexible, several-jointed flagellum. These alterations which give rise to the characteristic free-swimming larva, the trochophore, commence most clearly at about twenty hours after development has started and the animal is in the gastrula condition. Gastrulation is at first epibolic, but invagination soon occurs with a well-marked blastopore and a typical invagination gastrula is formed. A similar gastrula occurs in the development of the oyster. The trochophore of twenty-four hours is a round, strongly ciliated embryo with a stiff anteriorly pointing flagellum. The disappearance of the blastopore has not been clearly seen, but it apparently takes place in the position which will be ultimately taken up by the proctodæum.

At forty hours the gut is clearly marked and at forty-two hours the trochophore shows the following features. The body has elongated, there is a band of very large cilia encircling the apical plate, from the centre of which springs the flagellum. The stomodæum has arisen as an invagination just behind the apical plate. It is lined with well-developed cilia, the effective stroke of which is inwards. The stomach is oval and lined with large cells. The proctodæum arises at the same time as the stomodæum and is now connected with the posterior part of the stomach. The larva swims actively by means of the body cilia in a spiral, clockwise manner. The flagellum is directed anteriorly and appears to be used as a tactile organ.

In a forty-five hours' embryo the shell appears as a patch of thickened ectoderm in the postero-dorsal region. It grows inwardly and ultimately covers the mid-dorsal line with glandular cells. At forty-eight hours a single unpaired shell is secreted above this. A hinge line soon appears, and at sixty-nine hours the shell is nearly large enough to enclose the whole animal. This shell, which differs in form, composition and minute structure from the adult shell, is the prodissoconch or larval shell. It is homologous with the protoconch of cephalic molluscs.

By the time the prodissoconch is large enough to cover the body, the velum has appeared as the organ of locomotion. It is developed as a line of large vibrating cilia from the apical plate and from its surrounding tissue, and is provided with two pairs of retractor muscles which can withdraw the velum into the shell. The velum is highly sensitive and is very rapidly withdrawn if it is touched.

Wilson describes an embryo of 0·134 mm. and at the most, twelve days old, with a straight intestine, a large œsophagus leading from the mouth at the posterior border of the velum to a stomach with a cavity divided into two by a well-defined band of cilia. The pallial muscles, which are the first muscles of the adult to be formed, are present.

Metamorphosis is characterised by the degeneration of the velum, a change in external form and the greater development of the internal organs both in number and complexity.

The following is a brief account of the development of the organs, each one being treated separately:

The mantle covers the whole body except for the expanded velum before the trochophore stage is ended. The animal then shows the beginnings of lateral compression.

The adult shell commences as a secretion from the centre of each lobe of the mantle of a 0·274 mm. embryo. A 0·512 mm. embryo has a shell far larger than the prodissoconch, which persists finally as the periostracum of the adult umbones.

During transition the intestine becomes looped and at 0·27 mm. the digestive organ appears as a pair of lateral diverticula from the stomach.

After the pallial muscle the anterior adductor muscle is formed from large mesoblast cells. The posterior adductor muscle follows immediately, but the anterior one is far the larger to start with.

The foot appears as an ectodermal evagination into which mesoderm grows. It is at first wedge-shaped, highly contractile and covered with cilia and becomes elongated as its development continues.

The byssus gland appears as an invagination ; at 0·385 mm. the posterior adductor muscles of the byssus are present and at 0·512 mm. the anterior ones are also developed.

Lacaze-Duthiers (1856) first worked out the development of the gills, but the following is based on the later work of Rice. The first filaments to be formed are the anterior ones of the inner gill, which develop as rod-like papillæ. The earliest observed case was that of a specimen 0·30 mm. long when there were three filaments. Flexure of these filaments to form the ascending lamellæ was found in specimens 0·75 mm. long, when there were in all twelve filaments present. The outer filaments were not seen until three or four were already present in an embryo 1·40 mm. long with twenty filaments in the inner gills ; these first-formed outer filaments probably develop together. Flexure of these outer gills occurs at 1·60 mm. when there are twenty-five inner and fifteen outer filaments.

The later developed filaments start as transverse folds or ridges and not as papillæ, as do the earlier ones. These ridges are at first comparatively short with a uniform convex outline. They then elongate and become flat-topped. Differentiation occurs by constriction or by differential growth. The resultant gills are a larger outer and a smaller inner. The filaments are at first united by a continuous membrane of very loose connective tissue which later breaks down and leaves bridges only, which form the interlamellar junctions.

The kidney arises as a small group of mesoderm cells in front of the posterior adductor muscles in specimens 0·36 mm. long.

The nervous system is derived from thickenings of ectoderm. The cerebral ganglion is the first to be formed at the base of the velum in the trochophore; the pedal is found in 0·36 mm. long larvæ and the visceral in those of 0·385 mm. There is a connective between the visceral and the pedal ganglia in the young *M. edulis*. The eyes are formed when the first gill papilla appears. They arise as an ectodermal invagination which is later filled with brown granules. Wilson saw the heart beating in embryos 0·65 mm. long which had ten or eleven gill papillæ. The genital organs do not develop until metamorphosis is complete. Wilson found specimens 4 mm. long which contained follicles with developing ova.

Matthews made artificial fertilizations of *Mytilus edulis*. On May 21st she shook ripe sperms and ripe ova into separate bowls. At 12 noon she took a few drops of water containing the sperms and added it to the water in the bowl containing the ova. At 4 p.m. she noticed the presence of polar bodies and early stages of segmentation. Later she pipetted the ciliated trochospheres from the top of the bowl and put them in jars of 2 litre capacity with a few drops of Nitzchia culture. On July 22nd the beginning of the prismatic shell was seen, and on August 4th the velum was decreasing and the foot was becoming long, thin and active. On August 22nd the largest specimen was 0·74 mm. by 1·16 mm. and by October 4th all but one was fixed by the byssus.

At the end of the summer the larvæ are very abundant and very active in localities where the adults occur. For instance, M'Intosh says that the surface of St. Andrew's Bay swarms with young mussels, which settle on every available structure. Nelson has examined young specimens which were floating on the surface of the water with the umbo downwards. These had lost their velum and were small but fully formed mussels. They were supported by a bubble of gas which occupied the posterior part of the mantle cavity. This gas, which, owing to the difficulty of obtaining a sufficient quantity, Nelson did not identify, is not present in the attached forms of the same size. The young have been seen to hang by a byssus thread from the surface film, which can support individuals 4 mm. long. They can also move along the surface film by means of cilia. Nelson suggests that the ability to bridge over metamorphosis while remaining pelagic is an important factor in accounting for the wide distribution and abundance of *M. edulis.*

THE RATE OF GROWTH.

The rate of growth in *Mytilus edulis* is variously affected by the surroundings, of which the principal controlling factor is the food supply.

Williamson found that mussels in captivity, if ¾ inch long, grew ⅛ to ⅜ inch in two years, while 1-inch specimens added ⅜ inch, and 1½-inch specimens added $\frac{1}{16}$ to ¼ inch in the same time. This is, of course, slow. The shape was characteristic too, being thicker from side to side and narrower along the dorso-ventral axis than in free-living forms. In favourable localities a two-year-old mussel would be 2 inches long. At St. Andrew's a two-year-old mussel is 1¼ to 2 inches long and a three-year-old one 2 to 2½ inches long. In the Plymouth district young *M. edulis* may grow from 1¼ to 1½ or more inches long between April and November. Growth is slower in winter, but the following April when the mussel is a year old it may be up to 2 inches long.

An 18 months old mussel may be as much as 2¼ to 3¼ inches, but the average size is 2 inches long. Herdman says that the Bay of Aiguillon mussels spawn early in the spring. By the end of May the young are $\frac{3}{10}$ inch long, and are ready for transplanting by the end of July, when they are ¾ inch long. About a year later they are 1½ inches long and ready for the market, but the largest are 2 to 2½ inches long when they are eaten. In England a four-year-old mussel is ready for food or bait, and at this age it is 3 to 3½ inches long. M'Intosh reports that a male 1¼ inches long had fully formed sperms, and a female of 1⅓ inches had fully formed ova. I have examined specimens considerably smaller than this which had gonads with quite extensive ramifications in the mantle. Orton has found one-year-old mussels spawning naturally. The locality where the most rapid increase of growth to a large size occurs is that between low-water neap tides and low-water spring tides, on flats where there is sand and gravel with a rich muddy detritus.

Brandt found that the size is inversely proportional to salinity, and in the Kaiser Wilhelm Canal, where salinity decreases from west to east, there is a corresponding decrease in the size of mussels. Other factors, such as differences in food supply, may, however, be retarding growth.

A river bed is one of the best places from which to get young mussels for transplanting. Young specimens seem to settle higher up the shores than do the older ones. Herdman considers that an admixture of fresh water seems to be highly favourable for mussel culture, and this is borne out by other workers. Weidlt considers them essentially a brackish-water animal.

Coulthard, in his experiments to determine the effects of light, heat and temperature on growth, found that the growth rate is independent of the size of the animal and is only affected by the environment. A half light gives the maximum growth, while in darkness growth is lessened and in full light lessened still more. Exposure to daylight for more than twelve hours out of the twenty-four practically inhibits growth. The optimum temperature lies between 10° and 20° C. Bruce remarks that growth of the shell does not take place during and for some time after spawning.

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EXPLANATION OF PLATES.

Reference Letters.

A.A.M. = Anterior adductor muscle.
A.A.N. = Anterior adductor nerve.
A.A.S. = Anterior adductor scar.
A.B. = Aortic bulb.
A.B.R. = Anterior byssal retractor muscle.
A.BR.I. = Ascending lamella of inner gill.
A.BR.O. = Ascending lamella of outer gill.
A.B.R.S. = Anterior byssal retractor muscle scar.
A.F.C. = Ab-frontal cilia.
AFF.BR. = Afferent branchial vessel.
A.G.A. = Anterior gastero-intestinal artery.
A.L.V. = Anterior longitudinal vein.
AN. = Anus.
AN.S. = Anal siphon.
ANT.A. = Anterior aorta.
A.O.V. = Afferent oblique vein.
A.P.A. = Anterior pallial artery.
A.P.N. = Anterior pallial nerve.
A.P.V. = Ascending pallial vein.
A.S. = Abdominal sense organ.
AUR. = Auricle.
A.V. = Anastomosing vein.
A.V.A. = Anterior ventral artery.
A.V.C. = Auriculo-ventricular communication.

B. = Byssus.
B.A. = Byssus aperture.
B.C. = Blood corpuscle.
B.G. = Byssal gland.
B.M. = Byssal muscle endings.
B.N. = Branchial nerve.
BR.M. = Branchial membrane.
BU.N. = Buccal nerve.
B.V. = Branchial vessel.
BY.C. = Byssogenous cavity.

C.A. = Cœliac artery.
CÆC. = Cæcum.
C.B. = Ciliary band in mouth.
C.COMM. = Cerebral commissure.
C.F. = Cavity of the flanks.
C.G. = Cerebral ganglion.
C.J. = Ciliary junction (interfilamentar).
C.P.CONN. = Cerebro-pedal connective.
C.V.CONN. = Cerebro-visceral connective.

D.BR.I. = Descending lamella of inner gill.
D.BR.O. = Descending lamella of outer gill.
D.D. = Digestive duct.
D.F. = Dorsal velum.
D.G. = Digestive gland.
D.I. = Direct intestine.
D.L. = Dorsal lip.
D.P.N. = Dorsal pallial nerve.
D.R.B.N. = Dorsal retractor byssal nerve.
D.T.A. = Dorsal tentacular artery.
D.T.A.L. = Left branch of dorsal tentacular artery.
D.T.A.R. = Right branch of dorsal tentacular artery.

E.A. = Excretory aperture.
EFF.BR. = Efferent branchial vessel.
E.P.C. = External plicate canal.
EX.AP. = Exhalent aperture.

F. = Foot.
F.C. = Frontal cilia.
F.G. = Food groove.
F.S. = Depression in foot.

G.C. = Genital canal.
G.C.1-4. = Genital canals.
G.E. = Genital epithelium.
G.F. = Genital follicle.
G.I.A. = Gastro-intestinal artery.
GON. = Gonad.
GON.A. = Genital aperture.
GON.D. = Gonoduct.

H. = Hinge.
H.A. = Hepatic artery.
H.T. = Hinge teeth.
H.V. = Horizontal vein.

I.A. = Intestinal artery.
I.BR. = Inner gill.
I.L.J. = Interlamellar junction.
I.L.P. = Inner labial palp.
I.M.F. = Intrinsic muscles of foot.
I.M.S. = Intermuscular sinus.

I.P.A. = Intermediate pallial artery.
I.P.A.2. = Second intermediate pallial artery.
I.P.C. = Inner plicate canal.

L. = Ligament.
L.C. = Lateral cilia.
L.D. = Lateral diverticulum of stomach.
L.F.C. = Latero-frontal cilia.
L.P.G.A. = Left posterior gastero-intestinal artery.
L.R. = Ligament ridge.
L.R.A. = Left recurrent artery.
L.T.A. = Left terminal artery.
LU. = Lunule.

M. = Mouth.
MANT. = Mantle.
MANT.E. = Epithelium of mantle.
MANT.I. = Inner border of mantle.
MANT.M. = Middle border of mantle.
MANT.M.E. = Outer epithelium of middle border of mantle.
MANT.O. = Outer border of mantle.
MES. = Mesosoma.
M.G.A. = Mantle branch of posterior gastro-intestinal artery.
M.S. = Marginal sinus.
M.V. = Mesosomal vein.

N. = Nacreous layer of shell.
NE. = Nucleolus.
NU. = Nucleus.

O. = Ovum.
O.BR. = Outer gill.
ŒS. = Œsophagus.
O.L.P. = Outer labial palp.
OP.N. = Optic nerve.
OS. = Osphradium.
OT. = Otocyst.
OT.N. = Otocyst nerve.

PAL.C. = Pallial cavity.
P.A.M. = Posterior adductor muscle.
P.A.N. = Posterior adductor nerve.
P.A.S. = Posterior adductor muscle scar.
P.B.R. = Posterior byssal retractor muscle.
P.B.R.S. = Posterior byssal retractor scar.
P.C. = Pericardium.
P.C.V. = Plicate canal vein.
PD.A. = Pedal artery.
PD.G. = Pedal ganglion.
PD.N. = Pedal nerve.
P.D.P.N. = Posterior dorsal pallial nerve.
PER. = Periostracum.
PER.A. = Pericardial artery.
P.G. = Pericardial gland.
P.L. = Pallial line.
PL.M. = Pallial muscle.
P.L.V. = Posterior longitudinal vein.
P.M. = Plicate membrane.
P.N. = Pallial nerve.
P.P.A. = Posterior pallial artery.
P.PD.N. = Posterior pedal nerve.
P.P.N. = Posterior pallial nerve.
PR. = Prismatic layer of shell.
P.R.N. = Posterior renal nerve.
P.S. = Pallial siphon.
P.V.P.N. = Posterior ventral pallial nerve.

RECT. = Rectum.
REN. = Kidney.
R.I. = Recurrent intestine.
R.P. = Retractor pedis muscle.
R.P.C. = Reno-pericardial canal.
R.P.G.A. = Right posterior gastero-intestinal artery.
R.P.S. = Retractor pedis muscle scar.
R.R.A. = Right recurrent artery.
R.T.A. = Right terminal artery.

S. = Spermatozoa.
S.M. = Sperm mother cells.
S.N. = Siphonal nerve.
STOM. = Stomach.

T. = Testis.
T.S. = Transverse sinus.

U. = Umbo.

V. = Ventricle.
V.COMM. = Visceral commissure.
V.D. = Ventral diverticulum of stomach.
V.F. = Ventral velum.
V.G. = Visceral ganglion.
V.L. = Ventral lip.
V.R.B.N. = Ventral retractor byssus nerve.
V.T.A. = Ventral tentacular artery.
V.T.A.L. = Left ventral tentacular artery.
V.T.A.R. = Right ventral tentacular artery.
V.V. = Visceral vein.

[Except in the case of the transverse sections, the animal has been removed from its shell. All the drawings are those of a mature specimen, the shell of which measured about 3 inches long, with the exception of the sections which are those of a young and only partially mature form.]

Plate I.

Fig. 1. Inner surface of left valve of a shell which has been treated with caustic soda. × 1½.

Fig. 2. Hinge area of the right valve. × 3.

Fig. 3. Hinge area of the left valve of the same shell as fig. 2. × 3.

Fig. 4. Right lateral view of the muscles. The right half of the mantle and the entire visceral mass have been removed. The left pedal retractor has been cut short and the connective tissue and horizontal muscles of the foot have been partly dissected away to show the byssal gland. × 1½.

Plate II.

Fig. 5. The animal seen from the ventral side. The mantle has been cut short on the left side for the greater part of its length ; anteriorly it has been displaced over to the right of the specimen. The foot, which is half-contracted, has been pinned over to the same side, with a consequent twist in the pedal retractor and byssal muscles. The left gills have been cut away close to the gill axis. × 3.

Plate III.

Fig. 6. Ventral view of the mouth and commencement of the œsophagus. The inner palps have been cut across in order to remove the ventral lip, the position of which is shown by the dotted line. The digestive gland and ventral part of the œsophagus have also been dissected off. The outer palps have been cut short. × 4.

Fig. 7. Dorsal view of the alimentary canal. The mid-dorsal part of the mantle and the dorsal wall of the pericardium have been removed; the broken lines indicate where this was done. The digestive gland has been dissected away from the stomach and part of the intestine. In the posterior region the three parts of the intestine overlying the posterior adductor muscle have been separated from one another. The passage of the rectum through the ventricle is shown by a dotted line. The reno-pericardial sinus is seen where it has been cut in front of the afferent oblique vein, and the pericardial glands are seen surrounding the left auricle. × 1½.

Fig. 8. The stomach from the dorsal side. The whole of the dorsal wall has been removed and the digestive gland is not shown. × 4.

Fig. 9. Lateral dissection of the alimentary canal from the right side. The right half of the mantle has been removed almost entirely and the muscles of the same side cut short. The right labial palps have been cut away and a good deal of the digestive gland dissected off. The whole of the right and the anterior part of the left gills have been removed. The right cerebro-visceral connective is shown cut short. Ramifications of the gonad and the pallial muscles are not figured. × 1½.

PLATE IV.

Fig. 10. Entire animal from the left side to show the minor and major genital canals. The position of the main genital duct is shown by dotted line, as is also the genital canal from the mesosoma, which can be seen lying under the byssus muscles. The pallial nerves are also shown where they can be seen in the mantle. The posterior ventral pallial nerve is shown by a broken line where it runs below the posterior adductor muscle and in the visceral mass. × 1½.

Fig. 11. Part of a microscope section through a minor genital canal and a follicle in the mantle of a female. × 120.

Fig. 12. Microscope drawing of part of the mantle of a female to show the termination of a minor genital canal. × 50.

Fig. 13. Part of a microscope section through a minor genital canal in the mantle of a male. × 200.

Fig. 14. Posterior view of the animal to show the exhalent aperture, branchial membrane and the vela. × 1¼.

PLATE V.

Fig. 15. Dissection of the gastero-intestinal arteries seen from the dorsal side. The heart and pericardium have been removed. × 3.

Fig. 16. A microscope section drawn somewhat diagrammatically. The section is a longitudinal one taken through part of the mantle and visceral mass in the region of the left gill axis of a female. The outer gill lamina is shown in section and the inner one is entire. × 40.

Fig. 17. Transverse microscope section across adjacent gill filaments showing two interfilamentar junctions. × 280.

Fig. 18. The muscles of the foot.

a. Posterior surface. The byssus has been cut off and the gland can be seen through the muscles of the foot in the middle line. × 3.

b. Anterior surface. The superficial muscles have been removed. The most posterior of the right posterior byssal muscles is cut short and the other posterior byssal muscles are not shown. × 3.

PLATE VI.

Fig. 19. Right lateral view of the mantle of a specimen after injection of the arteries. A window has been cut in the mantle on the side of the pericardium and part of the latter has been removed. The position of some of the viscera is shown by dotted lines. A portion of the anterior ventral artery is shown and also some of the hepatic arteries; otherwise the vessels are superficial. The pericardial glands can be seen covering the auricle. × 1½.

Fig. 20. Part of the ventral surface of the animal to show the external surface of the left labial palps and their arteries. The gills are shown cut short. × 2.

Fig. 21. Part of the ventral surface of the animal to show the inner surface of left labial palps and their arteries. The gills have been cut short. The left anterior byssus retractor muscle has been cut. × 2.

Fig. 22. Dissection of the right recurrent artery and of the posterior part of the anterior ventral artery. The foot is very much contracted. The right pedal retractor muscle has been removed. The most posterior of the right posterior byssal muscles is cut and the other byssal muscles are not shown. × 6.

PLATE VII.

Fig. 23. Diagram of the origin of the anterior ventral artery. × 4.

Fig. 24. Postero-ventral region of right half of the mantle of an injected specimen to show the veins. The cut surface of the left half of the mantle where it joins the right by the branchial membrane is shown in the upper right-hand corner. The cut edge of the left gills is shown, but the right ones are not drawn. × 2½.

Fig. 25. Ventral view of mesosoma and part of gill axis and neighbouring veins of the right side of an injected specimen. The gills have been cut short. × 5.

Fig. 26. Transverse section through the middle of the animal cutting the heart. The section is treated as if it were oblique in that the auriculo-ventricular aperture is shown on the right and not on the left. The gills, except for their axes, are not shown, nor is the shell. × 25.

PLATE VIII.

Fig. 27. Diagram to show the circulation of the blood. All the principal veins are shown, some cut short, but the smaller vessels are much modified in that where a series occurs from the same origin, as in the mantle, plicate canals and kidney, only three or four are figured. The same applies to the smaller arteries, but here the larger ones are also made diagrammatic. The pallial arteries and the posterior gastro-intestinal arteries are only represented by one vessel each. × 2½.

PLATE IX.

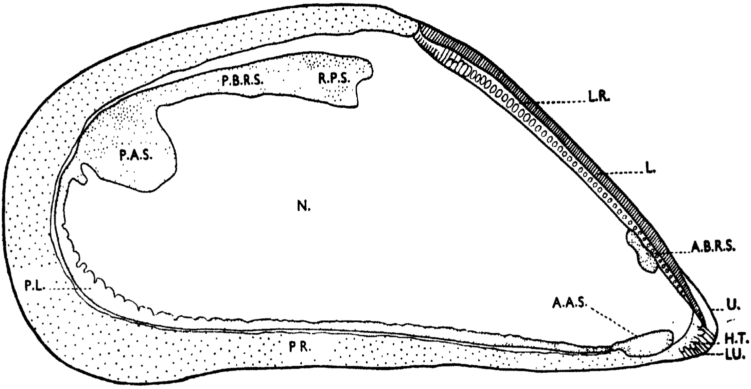
Fig. 28. Transverse section through a male taken at the level of the byssus. The drawing is somewhat diagrammatic. Owing to its reflexion, a section of the foot appears. × 25.

Fig. 29. Transverse section of the same specimen through the posterior region at the level of the termination of the direct and recurrent intestines. The section is somewhat diagrammatic, but, except for showing the branchial nerve and the visceral ganglion, which would not be present together, it has not been idealised. × 25.

PLATE X.

Fig. 30. Dissection of the nervous system from the ventral side. The left byssal muscles have been cut and in part removed. The gills have been cut short and the right labial palps removed. The heart and posterior viscera have been dissected away. The left half of the branchial membrane has been removed, also part of the posterior adductor muscle and inner part of the mantle of the same side.

The double broken line indicates the position of the exhalent aperture, in the centre of which are the vela. × 2.



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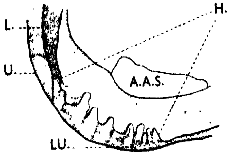

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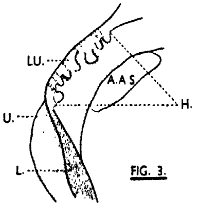

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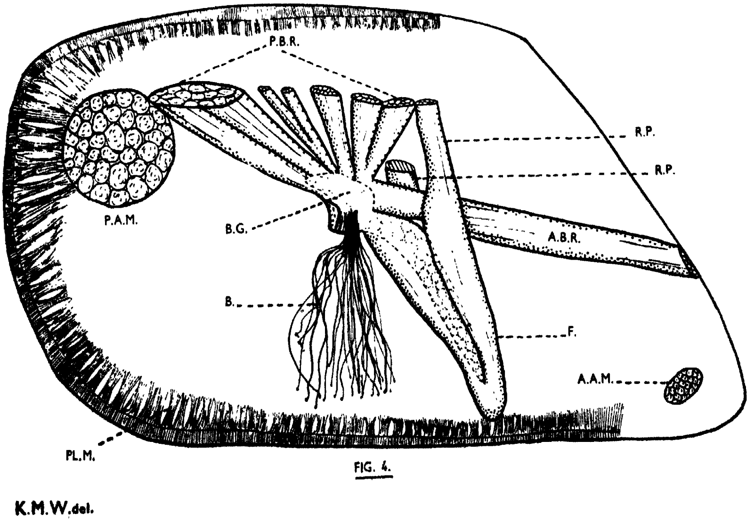

FIG. 4.

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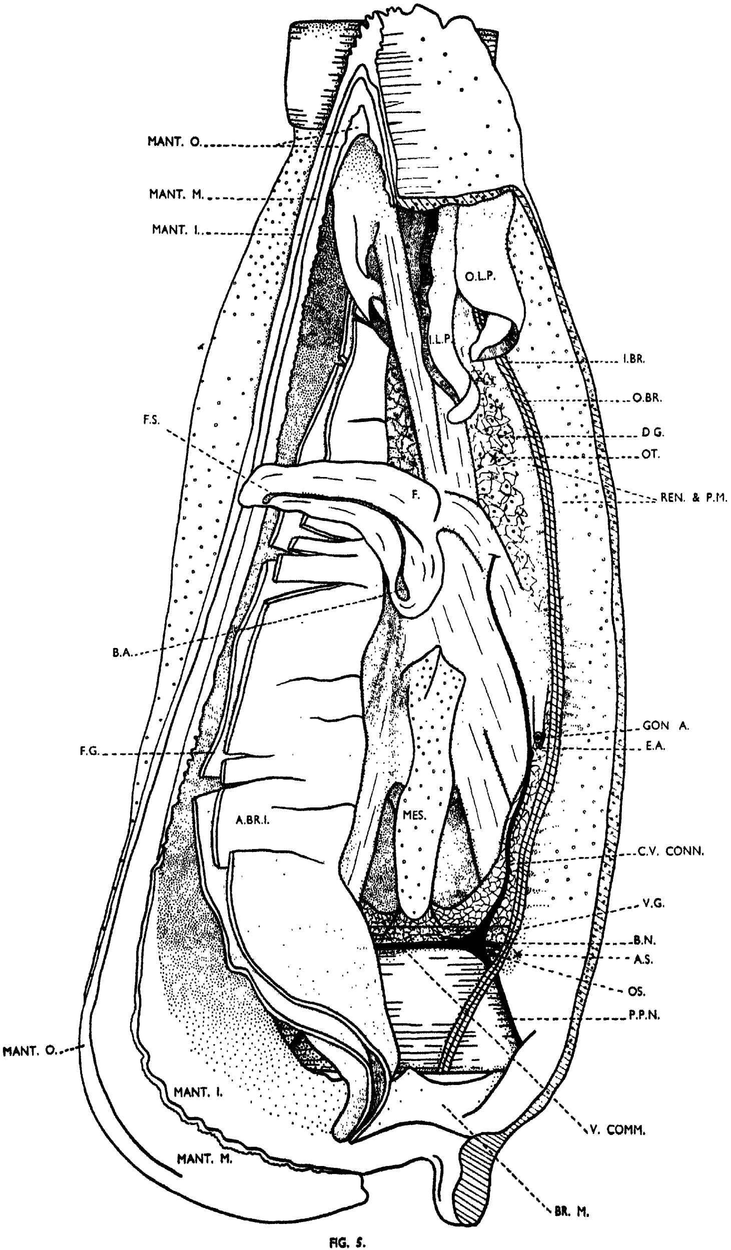

FIG. 5.

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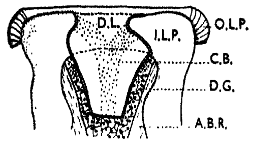

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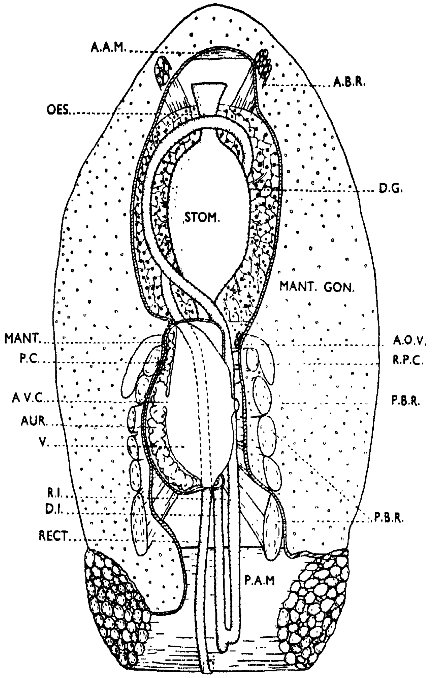

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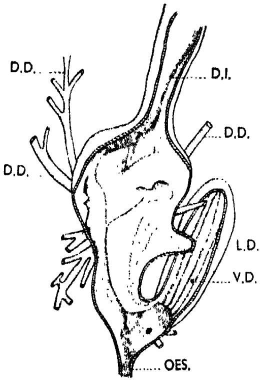

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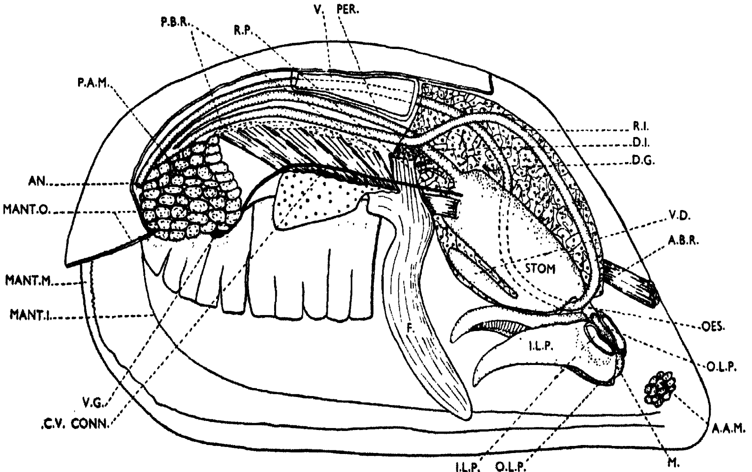

FIG. 9.

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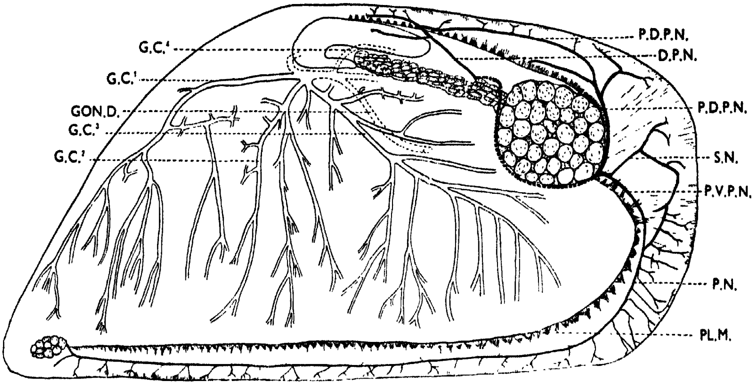

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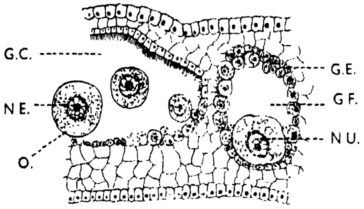

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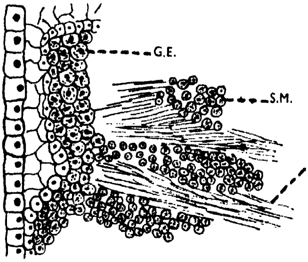

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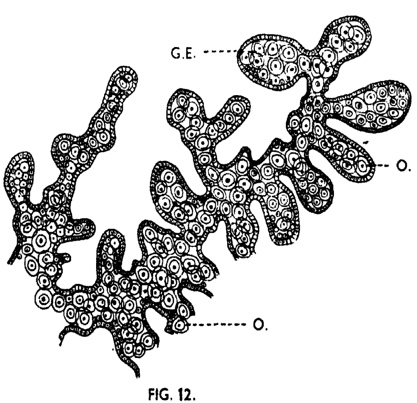

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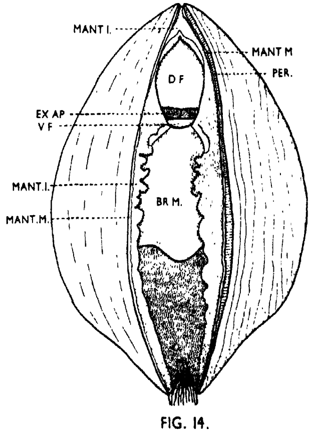

FIG. 14.

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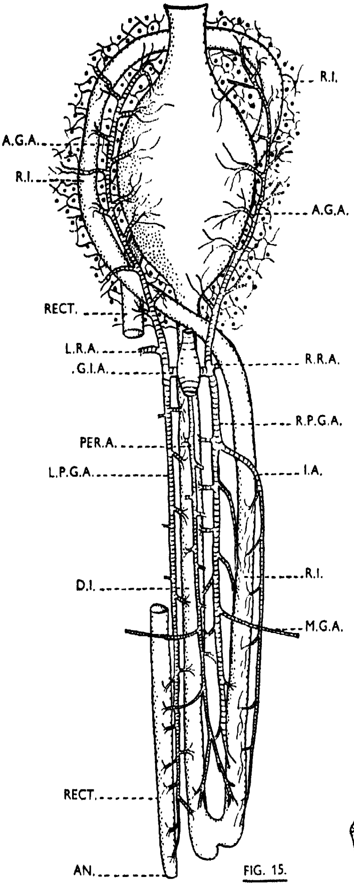

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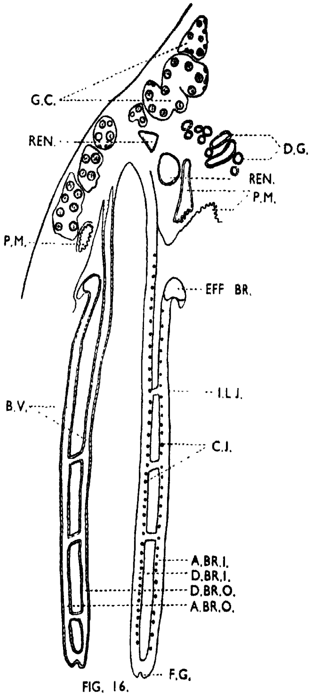

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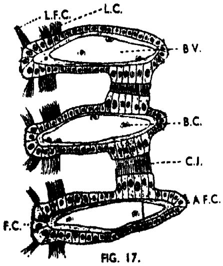

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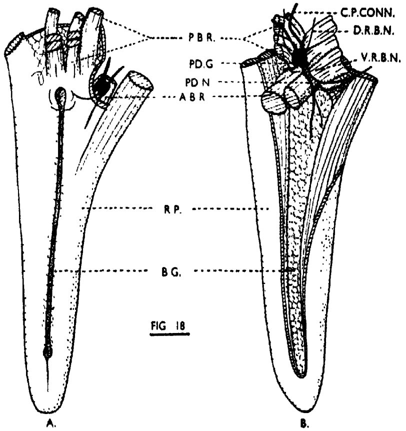

FIG 18

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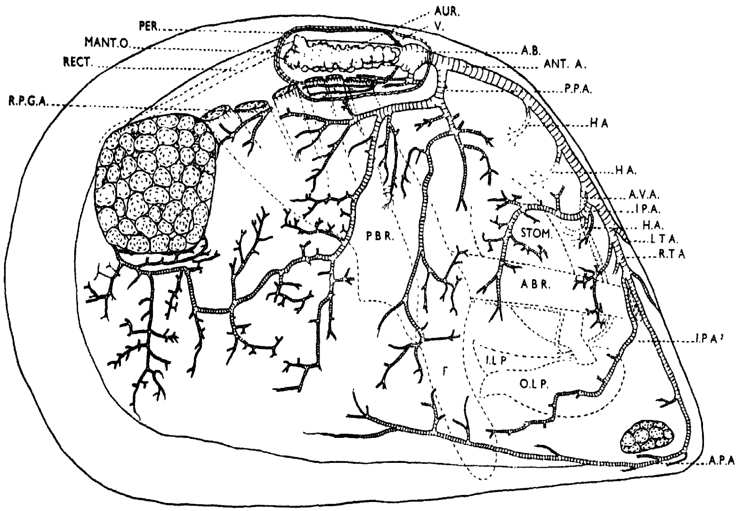

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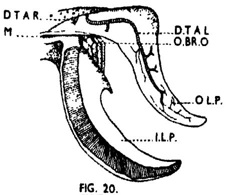

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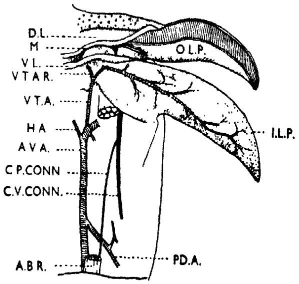

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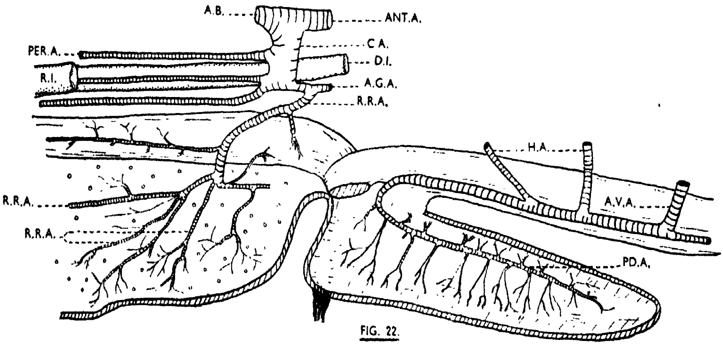

FIG. 22.

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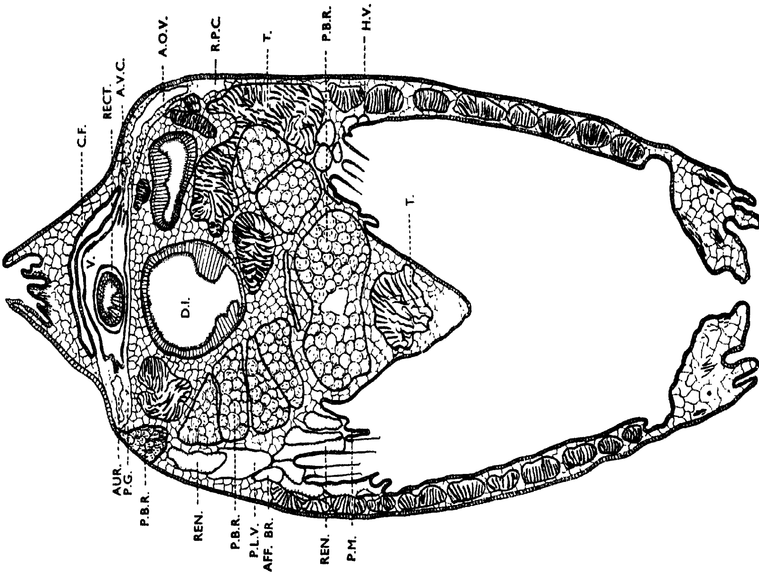

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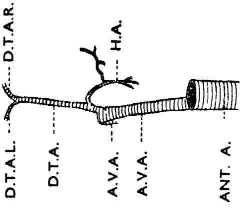

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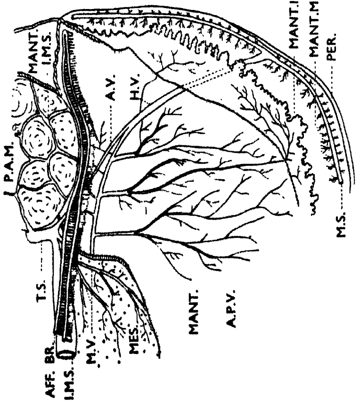

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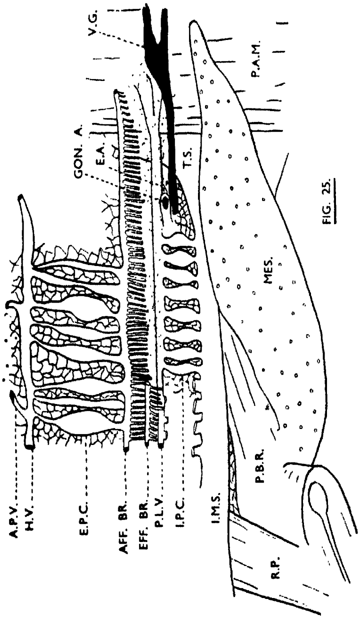

FIG. 25.

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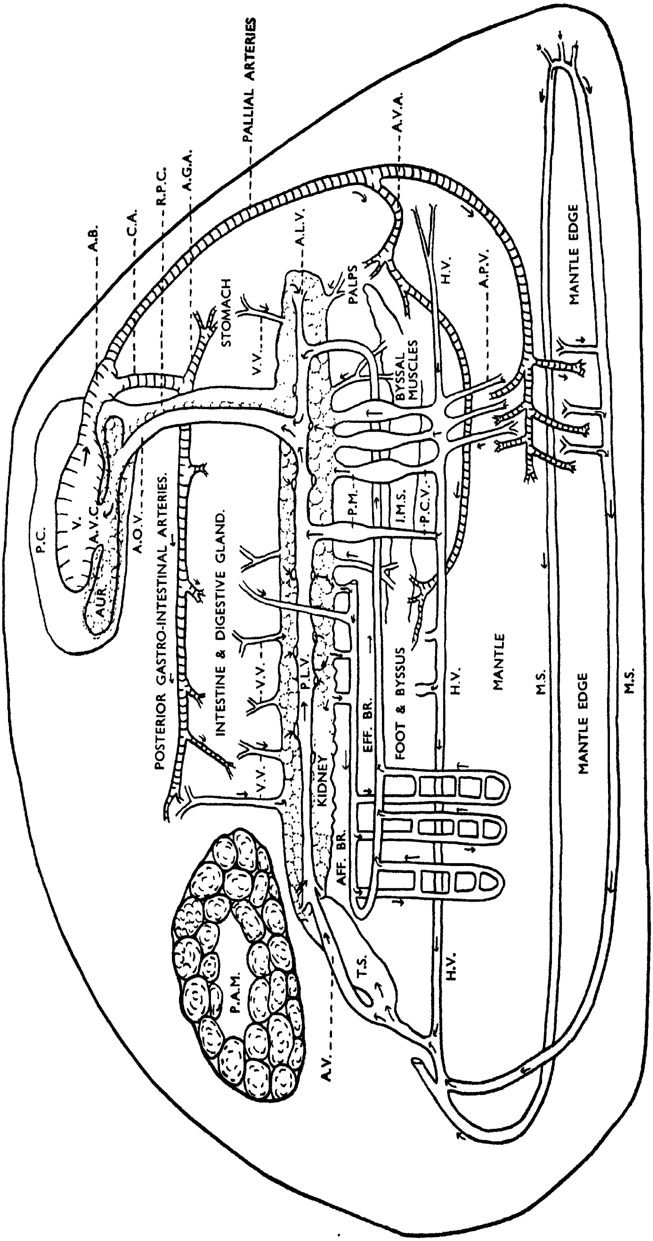

FIG. 27

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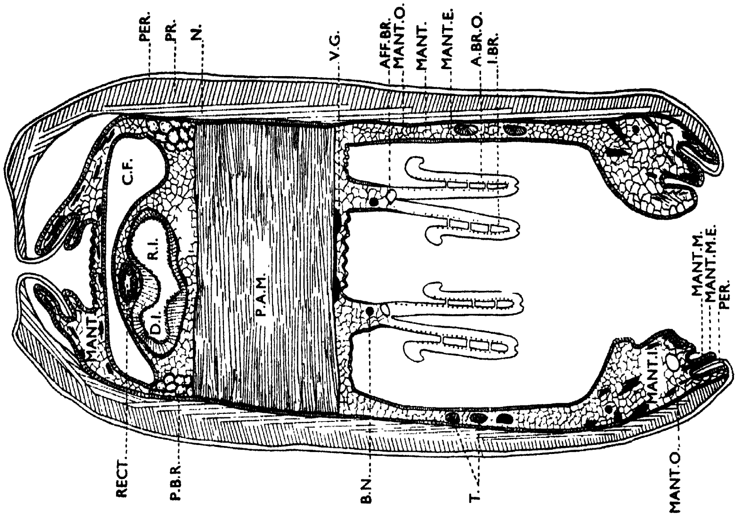

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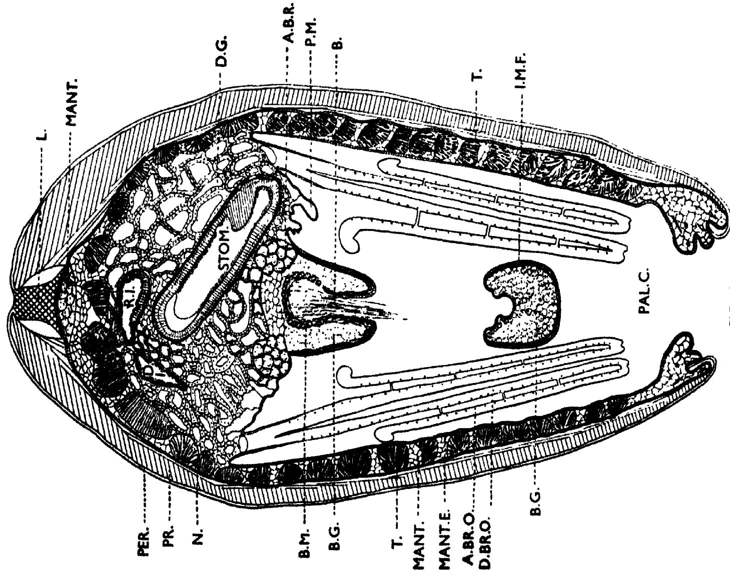

FIG. 28.

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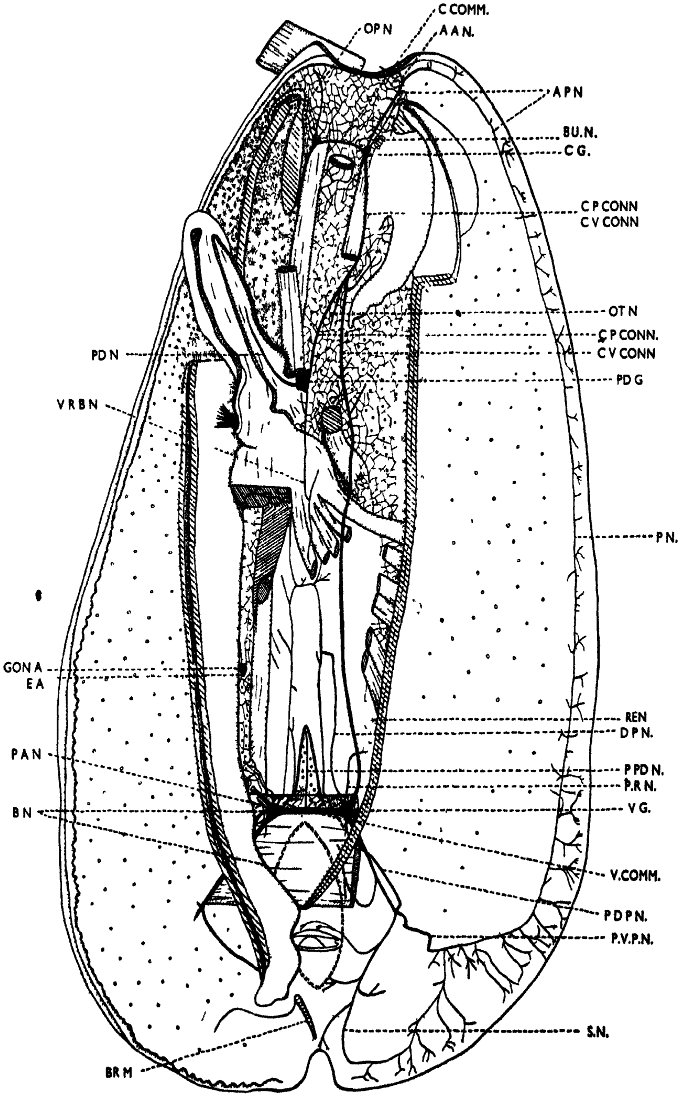

FIG. 30.

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